THE OSTEOLOGICAL DEVELOPMENT OF NINE SPECIES OF NOTOTHENIIDAE (PERCIFORMES: NOTOTHENIOIDEI)

by

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ABSTRACT. - The osteological development of nine species of nototheniids was investigated. All the species in general are characterized by the similar sequence of appearance of bones, except for *Pleuragramma antarcticum*. It is shown that the latest appearing bones are as a rule reduced in more derived species of the nototheniids and/or in advanced families of the notothenioids. The morphogenesis of certain characters of systematic value in general confirms validity of the subfamilies Nototheniinae, Trematominae and Pleuragramminae. Main trends of the skeletal development in the Nototheniidae subfamilies are considered.

RÉSUMÉ. - Développement du squelette de neuf espèces de Nototheniidae (Perciformes: Notothenioidei).

Le développement du squelette de neuf espèces de Nototheniidae a été étudié. Toutes ces espèces ont la même chronologie dans l'apparition des os, à l'exception de *Pleuragramma antarcticum*. Il est montré comme de règle que, chez les espèces les plus avancées de Nototheniidae et/ou chez des familles avancées de Notothenioidei les os qui apparaissent le plus tard ont une taille réduite. La morphogenèse de certains caractères de valeur systématique confirme la validité des sous-familles Nototheniinae, Trematominae et Pleuragramminae. Les principales tendances du développement du squelette chez les sous-familles de Nototheniidae sont considérées.

Key-words. - Nototheniidae, PSE, PSW, Antarctic, Skeleton, Ontogenesis, Morphogenesis.

Modern investigations of the early life history of Antarctic fishes include a wide variety of aspects concerning reproduction, growth, feeding and geographical distribution. The study of the external morphology of larvae and juveniles of notothenioids is the foundation for identification of species, now it is well worked up owing to the studies of North and White (1982), Efremenko (1983, 1987), Kellermann (1984, 1989, 1990) and North and Kellermann (1990). However, until recently the studies of other morphological features of larvae and juveniles, in particular the osteological features, were left out. Nevertheless, they are very important not only for the understanding of systematic and phylogenetic problems of notothenioids but also for the improving of our knowledge on the arising of morphological adaptations of the notothenioids to the extreme conditions of Antarctic habitats.

The aim of this research is the comparative analysis of the osteological development of nine species of nototheniids in relation to the problems of their systematic position and phylogeny.

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MATERIAL AND METHODS

The material used for our study belongs to the collection of larvae and juveniles of Antarctic fish at the Alfred Wegener Institute for Polar and Marine Research (Bremerhaven, Germany). These were obtained by several German Antarctic expeditions to the Scotia Sea and the Antarctic Peninsula between 1975 and 1987 (Kellermann, 1989). Additional material is from the Zoological Institute of the Russian Academy of Sciences. Altogether, 156 specimens, fixed in formaline were studied. They were cleared and stained following the method of Hollister (1934), modificated by Potthoff (1984). Series of 8 specimens of *Notothenia neglecta* Nybelin (16.5-359.3 mm SL), 23 spms of *Lindbergichthys nudifrons* (Lønnberg) (18.0-172.0 mm SL), 35 spms of *Gobionotothen gibberifrons* (Lønnberg) (11.5-274.3 mm SL), 28 spms of *Nototheniops larseni* (Lønnberg) (11.0-196.8 mm SL), 12 spms of *Lepidonotothen kempi* (Norman) (10.2-238.8 mm SL), 17 spms of *Pseudotrematomus scotti* (Boulenger) (14.0-168. 0 mm SL), 19 spms of *Trematomus newnesi* (Boul.) (15.7-217.3 mm SL), 7 spms of *Pagothenia borchgrevinki* (Boul.) (25.0-190.6 mm SL), 7 spms of *Aethotaxis mitopteryx* DeWitt (13.0-321.6 mm SL) were examined. Drawings were executed using a camera lucida attached to a stereo microscope and stained in Indian ink by A.V. Ljachova.

For the skull and pectoral girdle we follow the terminology of Harrington (1955) and of Jollie (1986). For the axial and caudal skeleton we follow the terminology of Monod (1968).

RESULTS

Subfamily Nototheniinae

Sequence of appearance of bones

In the neurocranium the appearance of bones in all studied species begins from the parasphenoid, frontal, basioccipital and exoccipital (Table I; Figs 1a, 2). Later the vomer, nasal, parietal and bones of the auditory region occur. After that, the supraoccipital, pterosphenoid, mesethmoid and lateral ethmoid appear (Figs 1c, 2c). The intercalar and basisphenoid occur later.

In the visceral skeleton, the early appearance of the upper and lower jaw bones occurs (Table I; Figs 3a, d, e); the maxilla, dentary and premaxilla appear before hatching. In the suspensorium first ossifications correspond to the quadratojugale, quadrate, symplectic, opercle; in the hyoid arch the ceratohyal and posterior branchiostegal rays; in the branchial arch the ceratobranchials (Figs 4a, 5a, 6a). The quadratojugale appears as a thin dermal bone on the ventral part of the hyomandibular-symplectic cartilage. After that the quadrate appears in the ventral part of the palatoquadrate cartilage, the quadratojugale spreading under the quadrate to the anterior edge of the palatoquadrate cartilage. Later both bones fuse in one bone, quadratojugal becoming the posterior process of quadrate. The similar appearance of the quadrate was noted in *Pleuragramma antarcticum* Boul. (Voskoboinikova *et al.*, 1994). We consider the dermal element as the homologue of the quadratojugal of lower osteichthyans following the view of Jollie (1986). Homology of this bone is supported by its dermal origin, position, relation to surrounding bones and earlier appearance comparing with quadrate. There is another point of view on the origin of posterior process of quadrate of Teleostei of connective tissue (Arratia and Schultze, 1991).

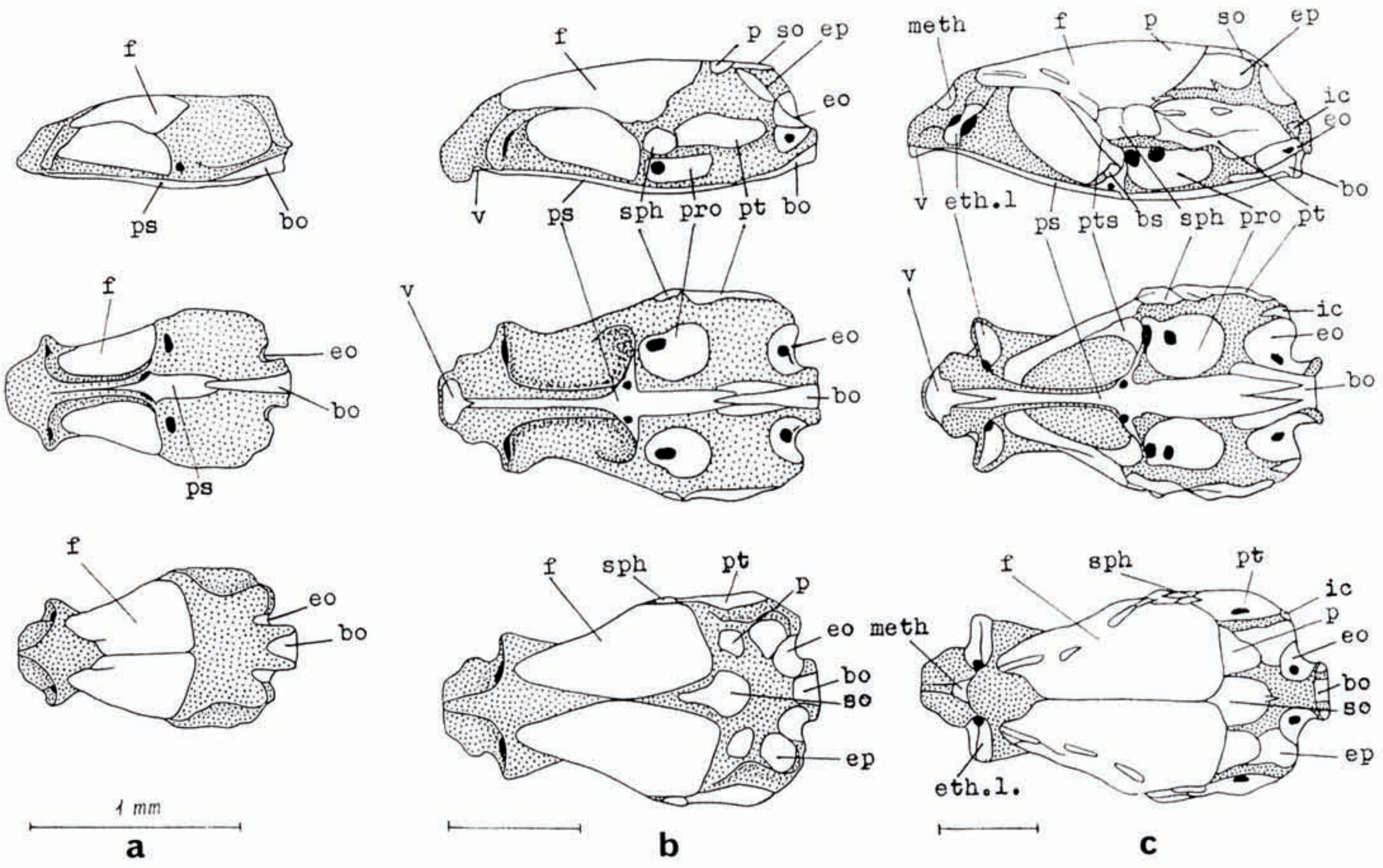


Fig. 1. - Development of the neurocranium in *Notothenia neglecta*, in dorsal (bottom), ventral (middle) and left lateral (upper) views. Standard lengths of specimens are: (a) 16.5 mm; (b) 24.0 mm: (c) 37.0 mm. bo: basioccipital; bs: basisphenoid; eo: exoccipital; ep: epiotic; eth.l: lateral ethmoid; f: frontal; ic: intercalar; meth: mesethmoid; p: parietal; pro: prootic; ps: parasphenoid; pt: pterotic; pts: pterosphenoid; so: supraoccipital; sph: sphenotic; v: vomer. Cartilage stippled, bone white.

Table I. - The appearance of bones in ontogeny of the nototheniids. 1 - *N. neglecta*, 2 - *G. gibberifrons*, 3 - *L. nudifrons*, 4 - *L. kempi*, 5 - *N. larseni*, 6 - *P. scotti*, 7 - *T. newnesi*, 8 - *P. borchgrevinki*, 9 - *A. mitopteryx*.

Bones	**Species**								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
mesethmoideum	33,0	25,0	35,0	35,2	44,0	38,0	54,7	32,5	-
lateral ethmoid	30,0	25,0	35,0	35,2	36,0	28,0	54,7	32,5	-
frontal	16,5	16,5	25,0	26,0	31,4	19,5	26,0	32,5	27,0
nasal	21,0	19,0	29,0	35,2	33,5	28,0	26,0	32,5	27,0
parietal	24,0	19,0	29,0	35,2	31,4	28,0	34,0	32,5	36,0
vomer	24,0	19,0	18,0	31,0	31,4	22,5	26,0	32,5	27,0
parasphenoid	16,5	16,5	18,0	26,0	18,2	14,0	11,0	25,0	13,0
pterosphenoid	30,0	25,0	37,0	35,2	33,5	28,0	54,7	34,0	-
prootic	24,0	19,0	29,0	35,2	31,4	28,0	30,5	34,0	-
sphenotic	24,0	25,0	25,0	35,2	31,4	22,5	34,0	32,5	-
pterotic	24,0	19,0	27,0	35,2	31,4	22,5	30,5	32,5	-
epiotic	24,0	25,0	29,0	35,2	31,4	22,5	34,0	32,5	-
intercalar	30,0	35,0	37,0	42,7	31,4	28,0	54,7	32,5	-
posttemporal	18,0	19,0	25,0	35,2	23,0	19,5	30,5	32,5	21,5
supraoccipital	24,0	25,0	29,0	31,0	31,4	28,0	54,7	32,5	-
exoccipital	16,5	19,0	25,0	26,0	24,2	19,5	30,5	32,5	27,0
basioccipital	16,5	16,5	18,0	26,0	18,2	19,5	15,0	25,0	13,0
maxillae	16,5	11,5	18,0	10,2	11,0	14,0	11,0	25,0	13,0
premaxillae	16,5	11,5	18,0	26,0	18,2	14,0	15,0	25,0	13,0
dentary	16,5	11,5	18,0	26,0	11,0	14,0	11,0	25,0	13,0
anguloarticular	16,5	16,5	18,0	26,0	18,2	14,0	15,0	25,0	27,0
retroarticular	16,5	16,5	18,0	26,0	18,2	14,0	21,0	25,0	27,0
palatine	24,0	19,0	27,0	35,2	31,4	28,0	30,5	32,5	-
quadrate + quadratojugal	16,5	16,5	18,0	26,0	18,2	14,0	22,0	25,0	27,0
ectopterygoid	24,0	19,0	28,0	35,2	31,4	28,0	30,5	34,0	-
entopterygoid	16,5	19,0	27,0	35,2	31,4	22,5	26,0	34,0	-
metapterygoid	24,0	19,0	27,0	35,2	31,4	22,5	26,0	32,5	-
hyomandibular	24,0	19,0	25,0	26,0	31,4	22,5	26,0	32,5	-
symplectic	16,5	16,5	18,0	26,0	18,2	16,0	22,0	32,5	27,0
interhyal	24,0	25,0	28,0	35,2	31,4	28,0	30,5	34,0	-
epihyal	24,0	19,0	25,0	35,2	31,4	22,5	30,5	32,5	36,0
ceratohyal	18,0	16,5	18,0	26,0	18,2	16,0	22,0	25,0	21,5
lower hypohyal	18,0	19,0	18,0	35,2	24,2	19,5	26,0	32,5	21,5
upper hypohyal	33,0	29,5	31,0	35,2	31,4	28,0	54,7	44,0	-
basihyal	24,0	25,0	27,0	35,2	31,4	22,5	54,7	34,0	36,0
urohyal	24,0	19,0	18,0	28,4	31,4	22,5	30,5	34,0	36,0
radii branchiostegi	16,5	11,5	18,0	26,0	18,2	16,0	11,0	25,0	21,5

Table I. - Continued.

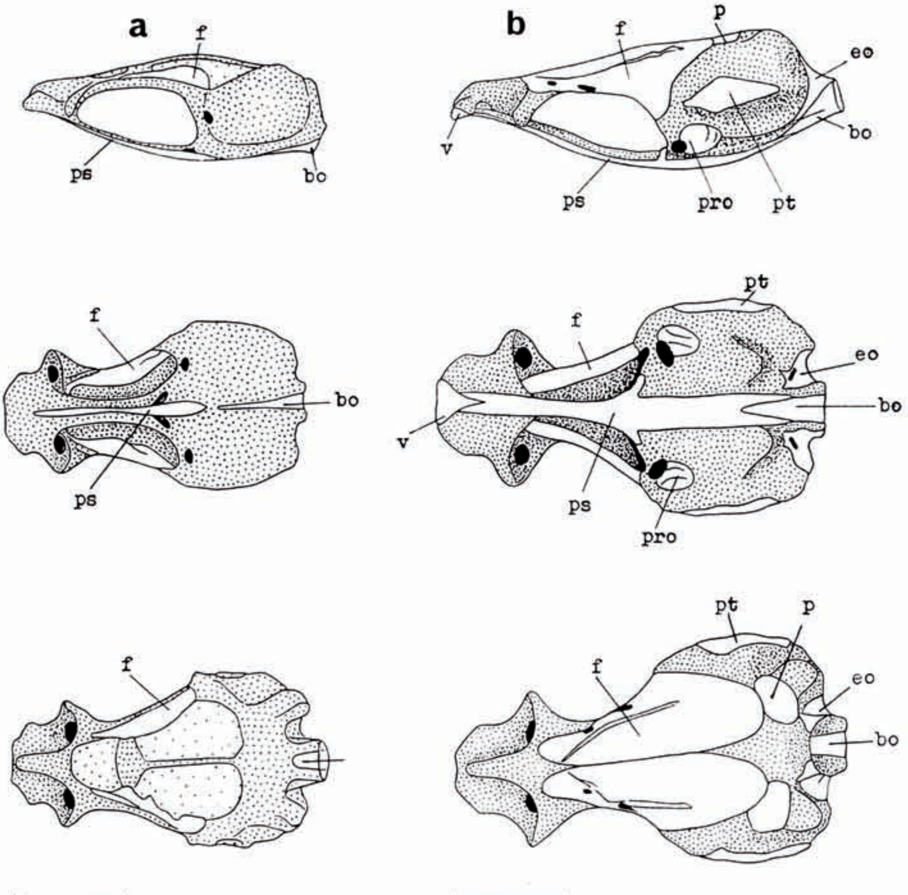
Bones	**Species**								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
basibranchial 1	37,0	35,0	39,0	35,2	40,0	22,5	54,7	44,0	-
2	33,0	33,0	37,0	-	36,0	22,5	54,7	-	-
3	24,0	25,0	28,0	35,2	31,4	22,5	54,7	44,0	-
hypobranchial 1	24,0	25,0	27,0	35,2	31,4	22,5	54,7	40,0	-
2	24,0	25,0	28,0	35,2	31,4	22,5	54,7	40,0	-
3	30,0	29,5	35,0	35,2	31,4	22,5	54,7	40,0	-
ceratobranchial 1-5	18,0	16,5	18,0	26,0	31,4	19,5	54,7	32,5	21,5
epibranchial 1	24,0	25,0	28,0	31,0	31,4	22,5	54,7	34,0	-
2	24,0	25,0	28,0	31,0	31,4	22,5	54,7	34,0	-
3	24,0	25,0	27,0	31,0	31,4	22,5	54,7	34,0	-
4	24,0	25,0	27,0	31,0	31,4	22,5	54,7	34,0	-
pharyngo-branchials 2-4	24,0	16,5	26,0	26,0	31,4	19,5	11,0	32,5	27,0
opercle	16,5	11,5	18,0	26,0	18,2	16,0	11,0	25,0	21,5
preopercle	16,5	16,5	18,0	31,0	20,8	19,5	22,0	32,5	21,5
interopercle	16,5	16,5	18,0	31,0	24,2	22,5	26,0	32,5	27,0
subopercle	16,5	16,5	18,0	31,0	18,2	22,5	22,0	32,5	21,5
lacrimal	24,0	19,0	18,0	31,0	31,4	19,5	30,5	32,5	13,0
dermosphenotic	24,0	26,0	28,0	35,2	40,0	28,0	54,7	38,0	-
infraorbitals 2	33,0	29,5	31,0	42,7	41,3	28,0	54,7	no	-
3	33,0	29,5	29,0	42,7	41,3	28,0	54,7	no	-
4	30,0	26,0	28,0	42,7	40,0	28,0	54,7	38,0	-
cleithrum	16,5	11,5	18,0	10,2	11,0	14,0	11,0	25,0	13,0
coracoid	24,0	22,0	27,0	35,2	33,5	28,0	54,7	42,2	36,0
scapula	24,0	25,0	28,0	35,2	41,3	28,0	54,7	44,0	36,0
radials 2	24,0	25,0	28,0	35,2	33,5	20,0	54,7	34,0	-
3	24,0	22,0	27,0	35,2	33,5	20,0	30,5	34,0	36,0
4	24,0	22,0	27,0	35,2	33,5	19,5	30,5	34,0	36,0
5	24,0	25,0	27,0	35,2	33,5	20,0	54,7	34,0	-
supracleithrum	18,0	16,5	18,0	28,4	23,0	16,0	22,0	32,5	21,5
urostyle	16,5	16,5	18,0	26,0	18,2	14,0	22,0	32,5	21,5
hypural 1	16,5	16,5	18,0	26,0	18,2	16,0	22,0	32,5	21,5
2	16,5	16,5	18,0	26,0	18,2	16,0	22,0	32,5	21,5
3	16,5	17,5	18,0	26,0	18,2	16,0	22,0	32,5	21,5
4	16,5	17,5	18,0	26,0	18,2	16,0	22,0	32,5	22,0
5	30,0							40,0	
parhypural	24,0	19,0	18,0	26,0	24,2	19,5	26,0	32,5	27,0
epurals 1-3	33,0	29,5	29,0	35,2	41,3	38,0	54,7	34,0	-

Later the preopercle, interopercle, hyomandibular, metapterygoid, entopterygoid and palatine appear in the suspensorium; the lower hypohyal, epihyal, basihyal and urohyal appear in the hyoid arch and the pharyngo-, epi-, hypobranchials and third basibranchial appear in the branchial arches (Table I; Figs 4a, 5a, b, 6b). The ectopterygoid, upper hypohyal, hypobranchial 3, basibranchials 1 and 2 occur latest (Table I; Figs 4b, c, 5b-d, 6b-d).

Among the infraorbital bones in all the studied species of the nototheniins the lacrimal appears first. After that the infraorbital 4 and dermosphenotic appear and infraorbitals 3 and 2 occur latest. The articulation between this bones has next following: the lacrimal with infraorbital 2, the infraorbital 3 with infraorbital 4, the infraorbital 4 with dermosphenotic, the infraorbital 2 with infraorbital 3.

In the pectoral girdle the cleithrum is first occurring bone, the supracleithrum appears later (Table I). After that the coracoid, radials and scapula ossify (Fig. 7). The radials occur as follow: the radial 4, 3, 2 and 5. Later the radial 2 fuses with the scapula.

Species of nototheniins are characterized by the occurrence of different numbers of interradial foramina during ontogeny. In *N. neglecta* two foramina appear between radials



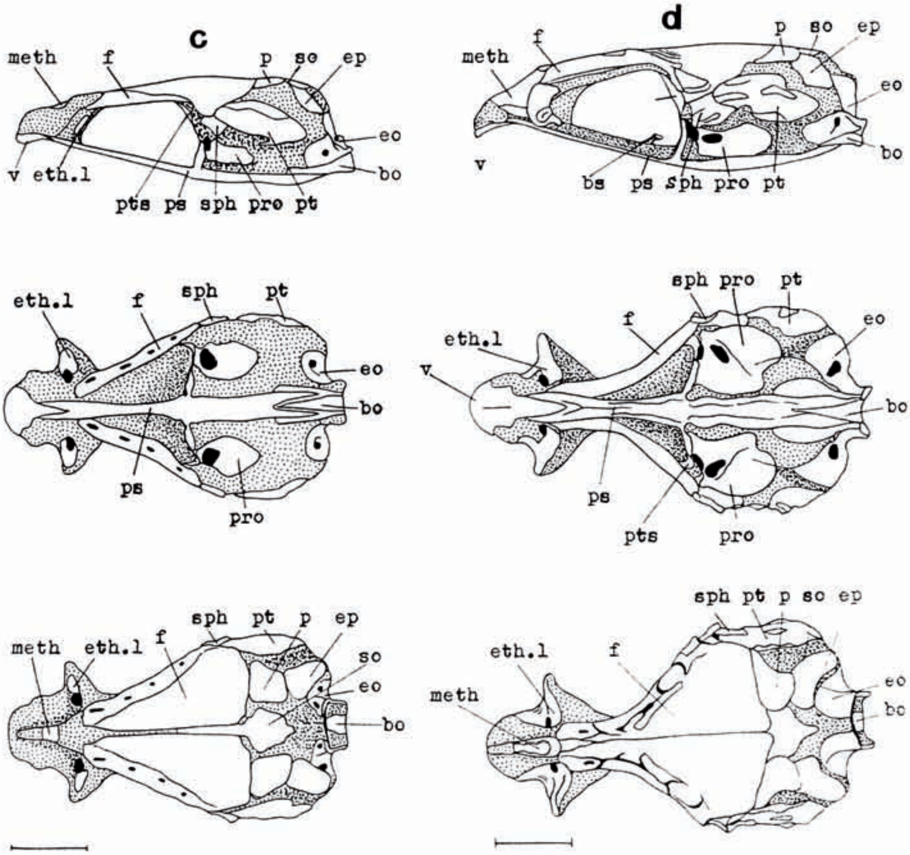


Fig. 2. - Development of the neurocranium in *Gobionotothen gibberifrons*, in dorsal (bottom), ventral (middle) and left lateral (upper) views. Standard lengths of specimens are: (a) 16.5 mm; (b) 19.0 mm; (c) 25.0 mm; (d) 32.5 mm. The labels as in figure 1.

3-4 and 4-5 (Fig. 7b, c). In *L. nudifrons* four foramina occur at 19 mm SL between radials 3-4 and radials 4-5 and at 29 mm SL between radials 2-3 and radial 2 and scapula, (this foramen is later included in the scapula). Similar sequence of appearance of interradial foramina is found in *L. kempi* and *N. larseni*. In *G. gibberifrons* three interradial foramina occur between the radials 2-3, 3-4 and 4-5. The number of the interradial foramina in adult nototheniins in general corresponds the number of foramina of early ontogeny (Balushkin, 1989).

In the axial skeleton of the nototheniins the urostyle ossifies first (Table I). Simultaneously, the neural arches ossify followed by the centra starting from the basioccipital posteriorly. In the caudal skeleton the ossification of the hypurals 1,2,3,4 and parhypural proceeds that of hypural 5 and of three epurals. The uroneural is the latest appearing bone. Later two haemal arches of the preural centra 1, 2 ossify followed by their respective neural arches. At this moment all vertebral centra are ossified, but some neural and haemal arches anteriorly to the preural centra still remain cartilaginous. In all the studied nototheniins the formation of vertebral centra arises as appearance of the

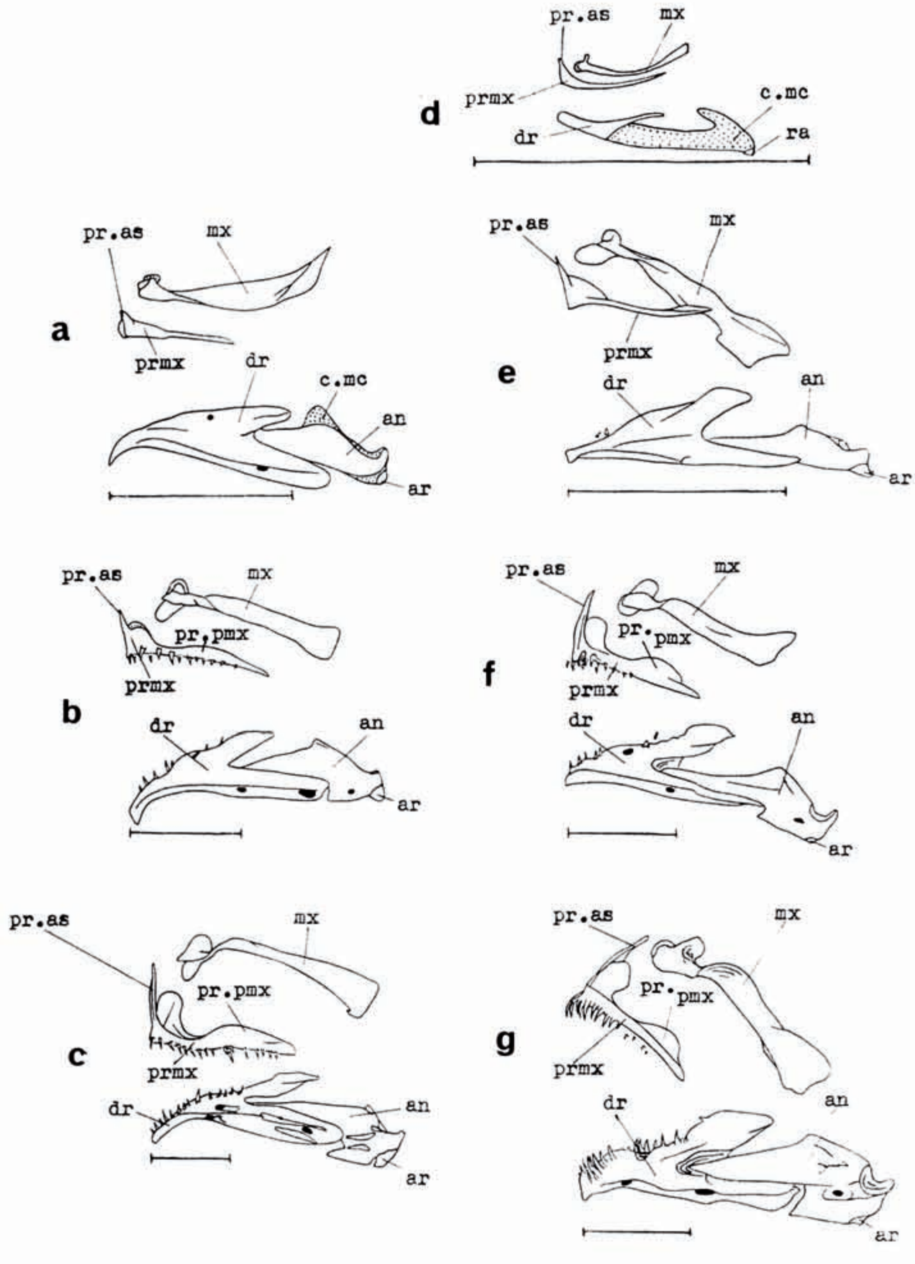


Fig. 3. - Development of the jaws in *Notothenia neglecta* (ac) and *Gobionotothen gibberifrons* (d-g), left lateral views. Lengths of specimens are: (a) 16.5 mm; (b) 24.0 mm; (c) 37.0 mm; (d) 11.0 mm; (e) 16.5 mm; (f) 24.0 mm; (g) 32.5 mm. an: anguloarticular; dr: dentary; mx: maxilla; prmx: premaxilla; pr.as: ascending process of the premaxilla; pr.pmx: postmaxillar process of the premaxilla; ra: retroarticular.

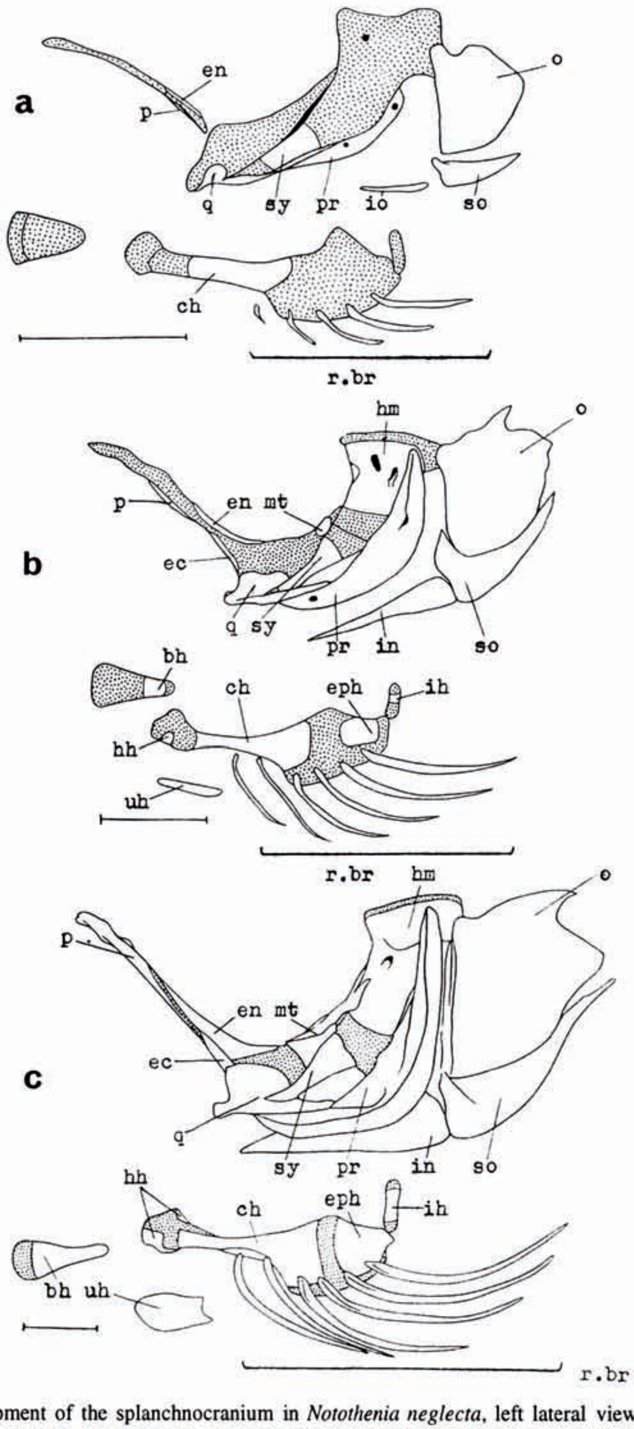


Fig. 4. - Development of the splanchnocranium in *Notothenia neglecta*, left lateral views. Lengths of specimens in (a-c) as in figure 1. bh: basihyal; ch: ceratohyal (= anterior ceratohyal), ec: ectopterygoid; eph: epihyal (= posterior ceratohyal); ec: ectopterygoid; en: entopterygoid; hh: hypohyals; hm: hyomandibular; ih: interhyal; in: interopercle; mt: metapterygoid; o: opercle; p: palatine; pr: preopercle; r.br: branchiostegal rays, q: quadrate; qjg: quadratojugal; so: subopercle; sy: symplectic; uh: urohyal.

saddle-shaped ossifications at the base of haemal archs which gradually dorsally grow over the notochord and join in rings at its dorsal surface.

Two ural centra were found in *L. kempi* (35 mm SL) and *N. larseni* (24.6 mm SL); in contrast three ural centra are in *N. larseni* (26.8 mm SL).

Between different species of the nototheniins few differences in the sequence of appearance of bones are found (Table I). *N. neglecta* and *G. gibberifrons* have the earlier appearance of the frontal than *L. nudifrons*, *N. larseni* and *L. kempi*. *L. nudifrons* is characterized by the earlier ossification of the sphenotic and pterotic comparing to *L. kempi* and *N. larseni*, and *G. gibberifrons* is characterized by the earlier appearance of the prootic and pterotic in comparison with other three species. In *N. larseni* the intercalar appears rather early together with other bones of the auditory region, and in other species it appears later. In *N. neglecta* the *ento*pterygoid occurs much more earlier than the metapterygoid, in other species these bones occur almost simultaneously.

Morphogenesis

Serious differences are found in the morphogenesis of different parts of the skeleton of studied species of the nototheniins. At the early stages of larval development (Voskoboinikova, 1994) all the species have rather compact shape of the neurocranium with the broad interorbital space, short and broad ethmoidal region. In *N. neglecta* this shape is conserved for life being characterized by the short mesethmoid, lateral ethmoid*s* and vomer (Fig. 1a-c; Balushkin, 1989, fig. 6). In *L. nudifrons* and *G. gibberifrons* (Fig. 2d) the anterior end of the frontal gradually lengthens and becomes narrower, so the interorbital width significantly decreases in adults. The characterized feature of *G. gibberifrons* is the formation of a projection of the interorbital region above the dorsal profile of the skull which is also well developed in adults (Balushkin, 1989, fig. 12c). The ethmoidal region of *L. nudifrons* and *G. gibberifrons* is longer than in *N. neglecta* from the early stages and gradually becomes more and more longer, and the anterior inclination of the ethmoidal region increases more than in *N. neglecta* on account for the sharp ventral curve of the head of the vomer. In *N. larseni* and *L. kempi* the interorbital width also decreases during ontogeny. The length of the ethmoidal region in both species is longer than in other nototheniins already at the early stages of the larval development and increases more strongly, in particular in *N. larseni*. The anterior inclination of the ethmoidal region in *L. kempi* and *N. larseni* increases less than in other species, and in adults of *N. larseni* does not approach the dorsal level of the interorbital space in comparison with other nototheniins.

All the studied nototheniins are characterized by the early appearance and fast development of the ascending processes of the parasphenoid which in adults reach the trigeminal nerve foramen (except for *N. larseni*).

The nototheniins are differentiated by characters of the structure of the splanchnocranium already at the early stages of development. So, *N. neglecta* at 24 mm SL has the large postmaxillary process of the premaxilla; large, sharp conical teeth on the jaws, ceratobranchial 5 and pharyngobranchials; palatine with a large head; square hyomandibular; large dorsal process of the opercle; well developed interstitial part of the preopercle; shortened posterior end of the subopercle (Figs 3, 4, 6). In ontogeny the enlargement of width of most bones proceeds, the dorsal ridge of the metapterygoid, hooked process of the hyomandibular, suture between the epi- and ceratohyal developing. In *L. nudifrons* at 26 mm SL well developed ascending and postmaxillary processes of the premaxilla appear. Teeth are rather small and sharp. The preopercle has a lengthened

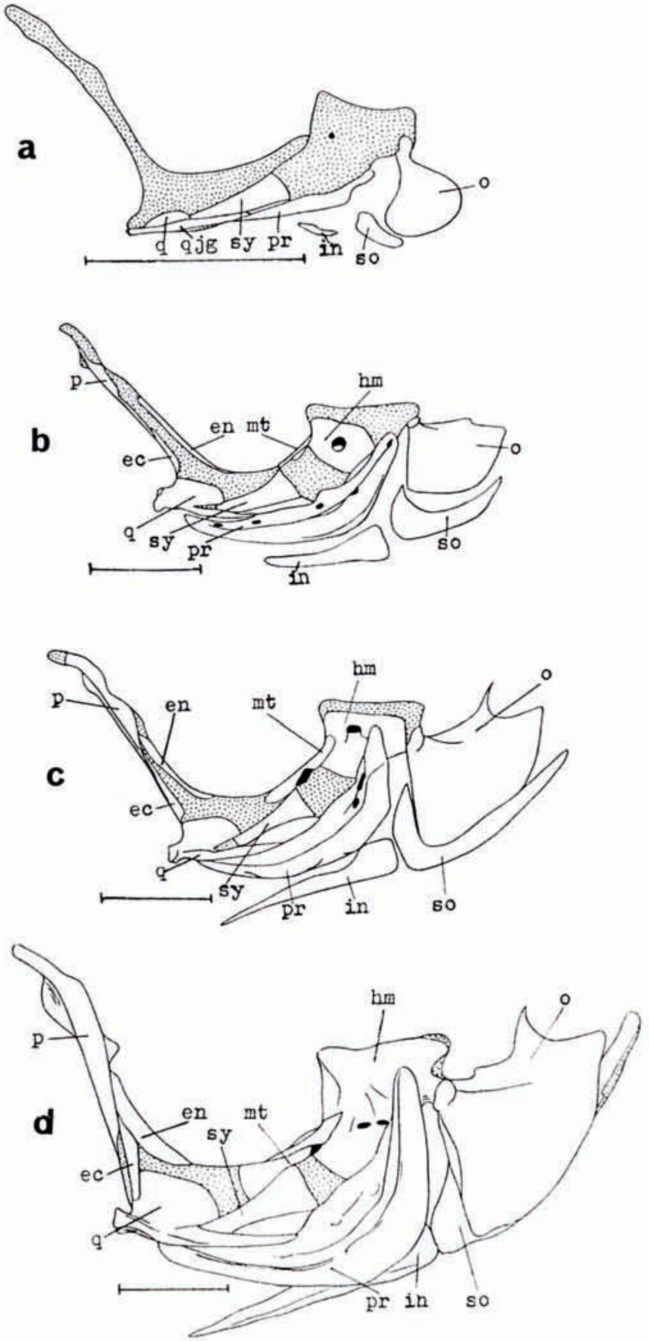


Fig. 5. - Development of the suspensorium in *Gobionotothen gibberifrons*, left lateral views. Lengths of specimens in (a)-(d) as in figure 2. The labels as in figure 4.

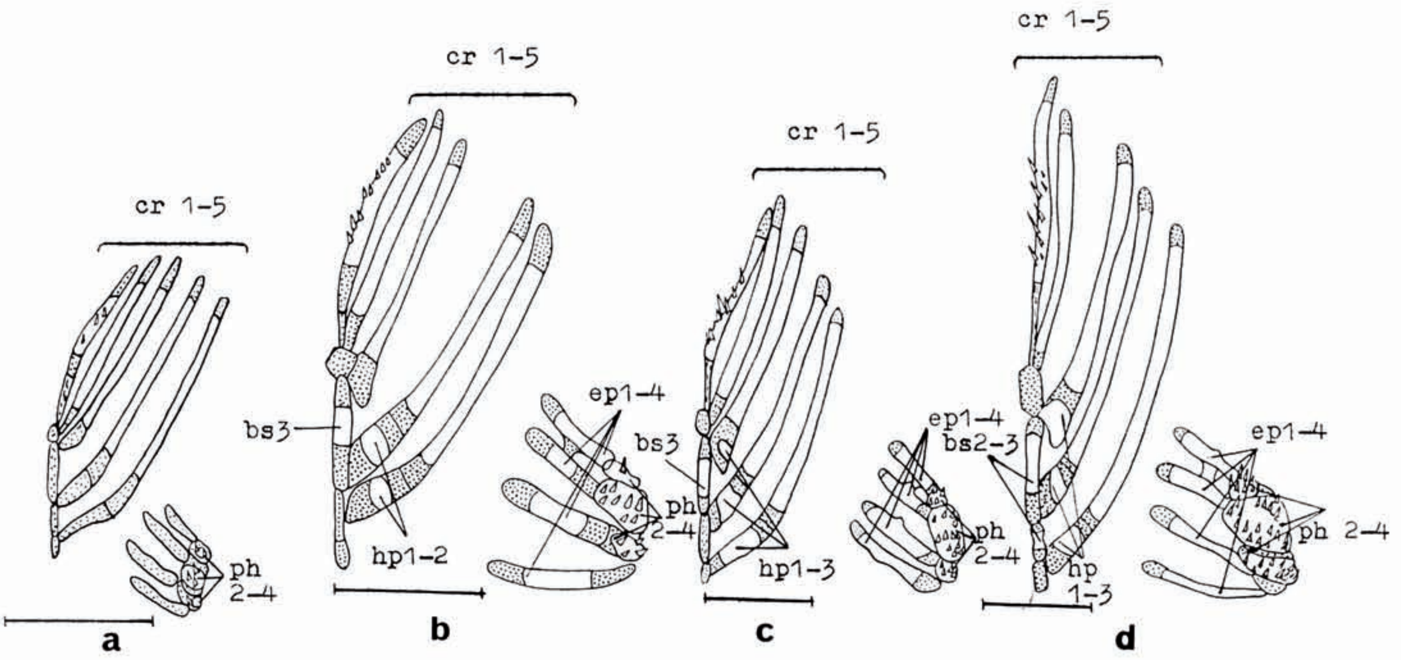


Fig. 6. - Development of the branchial skeleton of *Notothenia neglecta*, dorsal views for ventral parts of arches, ventral views for dorsal parts of arches. Lengths of specimens are: (a) 16.5 mm; (b) 24.0 mm; (c) 30.0 mm; (d) 37.0 mm. bs: basibranchial; cr: ceratobranchial; ep: epibranchial; hp: hypobranchial; ph: pharyngobranchial.

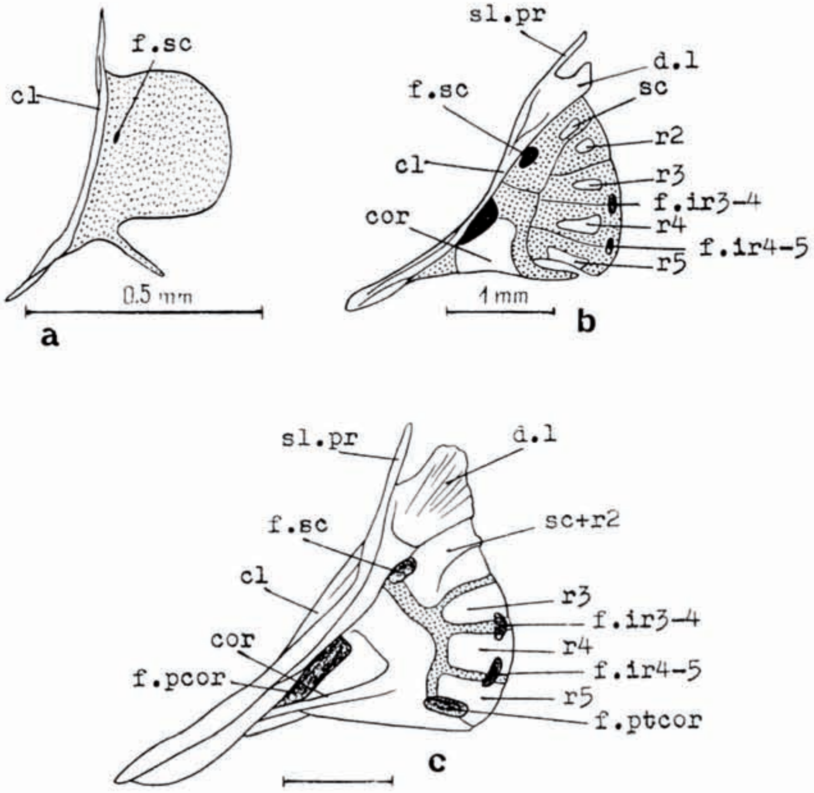


Fig. 7. - Development of the pectoral girdle and pectoral radials in *Notothenia neglecta*, left lateral views. Lengths of specimens are: (a) 16.5 mm; (b) 24.0 mm, (c) 60.0 mm. cl: cleithrum; cor: coracoid; r: radial; sc: scapula; d.l: dorsal lobe of the cleithrum; f.ir: foramen interradial; f.pcor: precoracoid foramen; f.ptcor: postcoracoid foramen; f.sc: foramen scapular; sl.pr: spine-like process of the cleithrum.

horizontal branch and a small interstitial part. The subopercle attaches the dorsal edge of the opercle already at 29 mm SL. During ontogeny of *L. nudifrons* there is no significant enlargement of width of the bones. *G. gibberifrons* at 11.5 mm SL has the ascending process of the premaxilla well developed (Fig. 3d) and the articulary and postmaxillary processes of the premaxilla appear at 16.5 mm SL. At this length, the first teeth on the jaws occur; they are long and a little curved as in adults. In larvae at 19 mm SL there are the rather broad palatine, hyomandibular and preopercle with the long horizontal limb. In comparison with *N. neglecta* all the bones are lower and longer (Figs 4, 5). The dorsal process of the opercle is very small and thin as in adults (Balushkin and Voskoboinikova, 1979). At 32.5 mm SL the considerable broadening of the palatine and the interstitial part of the preopercle along its horizontal limb and lengthening of the posterior process of quadrate were found. Later the broadening of bones in horizontal direction goes on, the premaxilla obtains the very high ascending process and the dorsal ridge of the metapterygoid appears. The development of the splanchnocranium of *L. kempi* is rather similar to

L. nudifrons, except for the arising of the rather low ascending and postmaxillary processes of the premaxilla and broadening of the hyomandibular vertically (Balushkin and Voskoboinikova, 1979). In *N. larseni* of 18 mm SL the postmaxillary process of the premaxilla is well developed as in adults. Small and villiform teeth appear at 33.5 mm SL and conserve their shape during ontogeny. Most of bones of the splanchnocranium, including the palatine, pterygoids, hyomandibular, preopercle, epi- and ceratohials and branchials, are characterized by the weak ossification in larvae and in adults of *N. larseni*.

It can be noted some general features in the shape of the splanchnocranium of the nototheniins at the early stages, such as the small highness of the suspensorium, horizontal position of the preopercle, sloped position of the anterior edge of the suspensorium which during ontogeny becomes more vertical.

In most of the nototheniins in the caudal skeleton each cartilaginous hypural ossifies into a bony hypural. Later bony hypurals 1 and 2 fuse in all the species, hypurals 3 and 4 fuse in *L. kempi* at 35 mm SL and in *G. gibberifrons* at 25 mm (Fig. 8f). Among the studied nototheniins *G. gibberifrons* is the only species in which the cartilaginous hypurals 1 and 2 fuse and only one bony hypural (1+2) appears in the hypaxial lobe (Fig. 8).

Subfamily Trematominae

Sequence of appearance of bones

In the trematomins the sequence of appearance of bones of the neurocranium in general corresponds to that of nototheniins (Table I; Fig. 9). Some differences among the three studied species of trematomins are noted in the appearance of the exoccipital. The exoccipital occurs in *T. newnesi* much more later than basioccipital comparing to other species. In *P. scotti* the frontal occurs simultaneously with the occipital bones, earlier than in *T. newnesi* and *P. borchgrevinki*. In *P. borchgrevinki* the late appearance of the nasal is noted.

In the splanchnocranium of the trematomins the same bony elements as in the nototheniins appear earliest (Table I; Figs 10a, 11a). The palatine, ectopterygoid, inter-, basi-, urohyal, upper hypohyal and branchials are characterized by the latest appearance (Fig. 11b).

The sequence of appearance of the infraorbitals of *P. scotti* and *T. newnesi* repeats the nototheniins. But in *P. borchgrevinki* there is no appearance of the infraorbitals 2 and 3, so in adults there is a large interruption in the infraorbital canal (Andriashev and Jakubowski, 1971).

The sequence of appearance of the bones of the pectoral girdle is very similar to that of nototheniins. The studied species of the trematomins show differences in the formation of the interradial foramina. In *T. newnesi* firstly three foramina occur among which the most dorsal foramen between the radials 2 and 3 disappears later. At 30.5 mm SL the small foramen into the radial 4 occurs. So, in adults of *T. newnesi* there are three interradial foramina between radials 3-4 and 4-5 and into the radial 4. In *P. scotti* and *P. borchgrevinki* the same three foramina previously occur at the early stages, a fourth small foramen at the base of the galanoid process (Balushkin, 1984) of the scapula and a fifth foramen into the radial 4 add later. The foramen between the radials 2 and 3 also disappears in adults, so they have four interradial foramina.

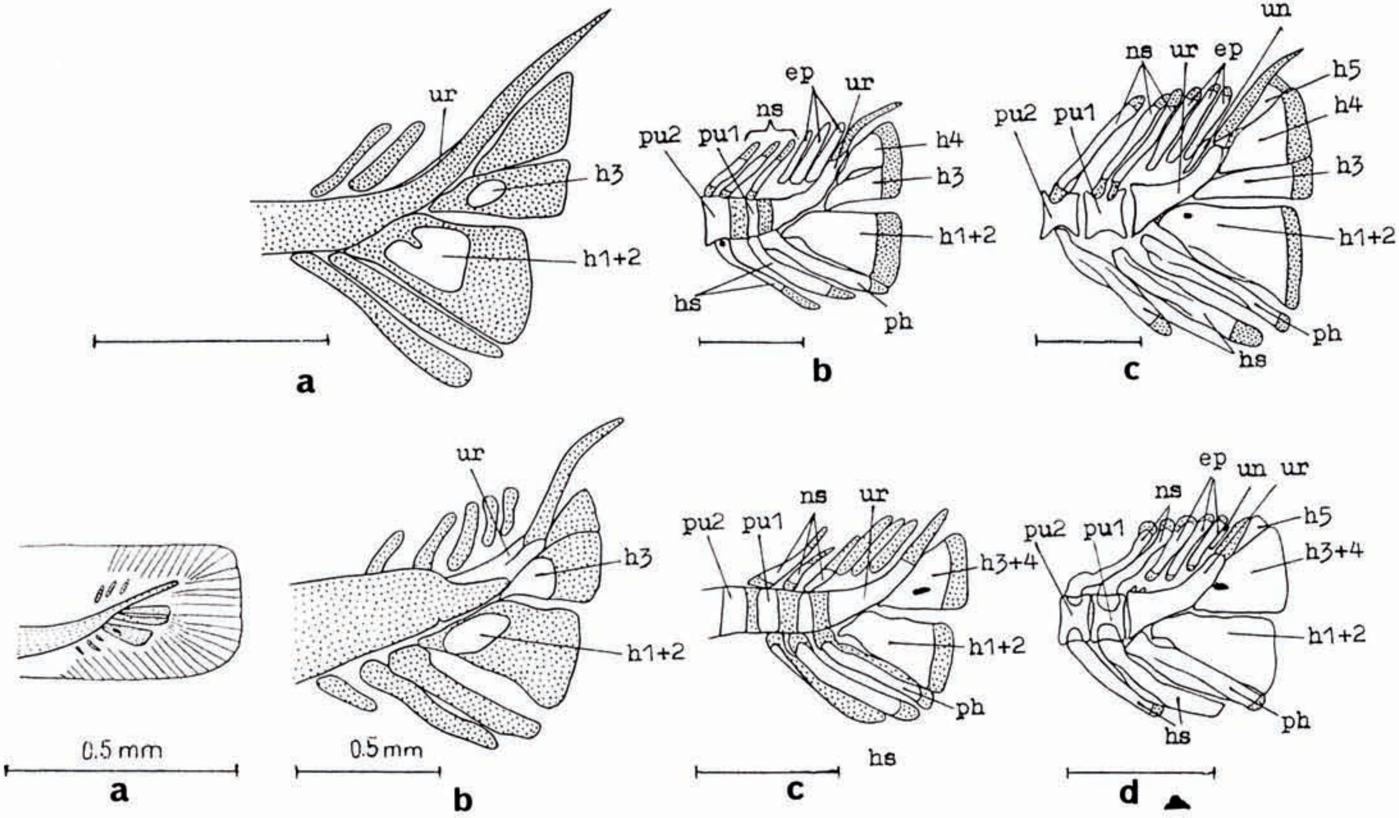


Fig. 8. - Development of the caudal skeleton in *Notothenia neglecta* (a-c) and *Gobionotothen gibberifrons* (d-g), left lateral views. Lengths of specimens are: (a) 16.5 mm, (b) 29.0 mm, (c) 32.5 mm, (d) 11.5 mm, (e) 16.5 mm, (f) 25.0 mm, (g) 32.5 mm. ep: epural; hs: haemal spine; h: hypural; ns: neural spine; ph: parhypural; pu: preural centrum; un: uroneural; ur: urostyle. Urostyle stippled.

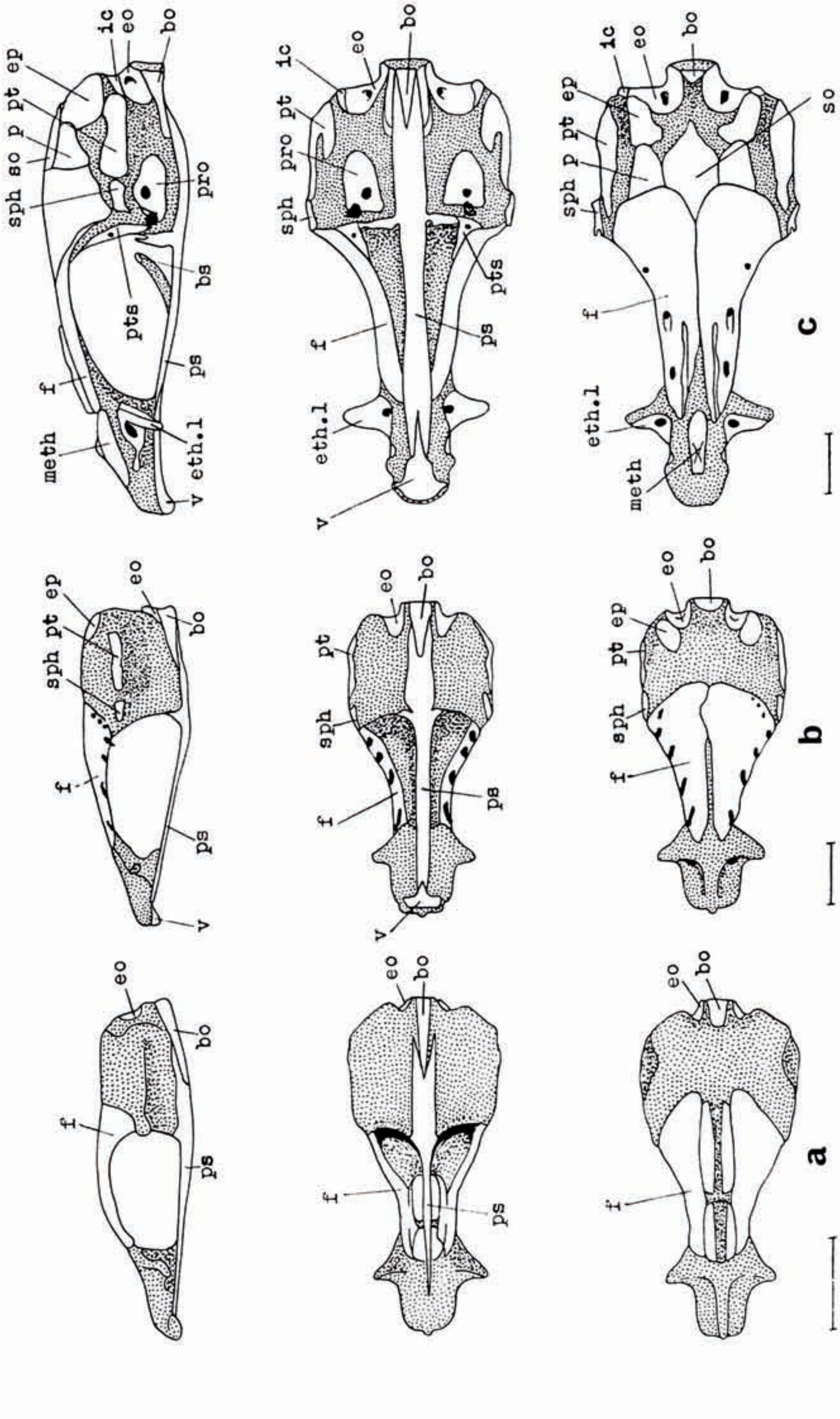


Fig. 9. - Development of the neurocranium in *Pseudotrematomus scotti*, showing dorsal (bottom), ventral (middle) and left lateral (upper) views. Standard lengths of specimens are: (a) 19.5 mm, (b) 22.5 mm, (c) 38.0 mm. The labels as in figure 1.

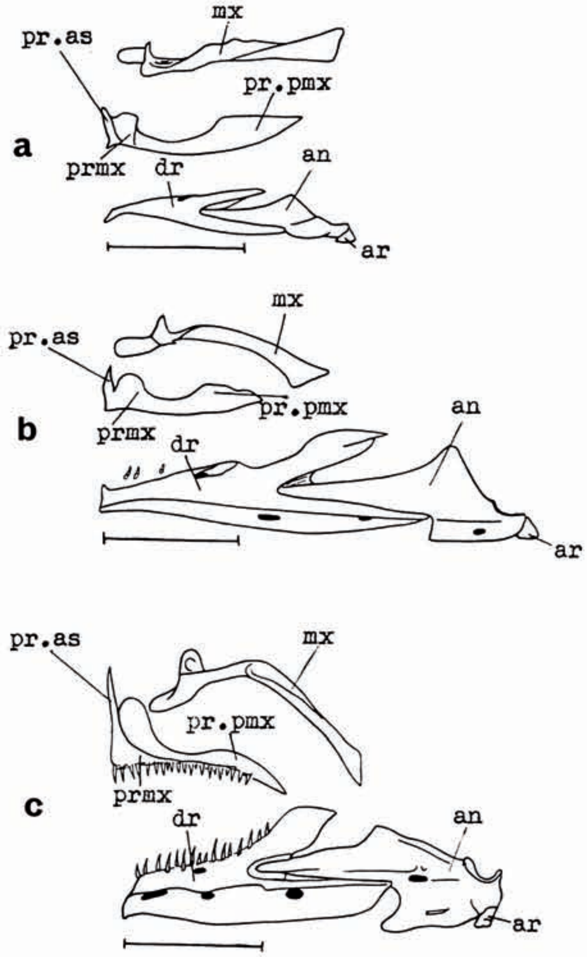


Fig. 10. - Development of the jaws in *Pseudotrematomus scotti*, left lateral views. Lengths of specimens as in figure 9. The labels as in figure 3.

The ossification of the axial skeleton of the trematomins corresponds in general to that of nototheniins. However, *P. scotti* and *P. borchgrevinki* differ from the most nototheniins (except of *L. kempi* and *G. gibberifrons*) and *T. newnesi* in that hypurals 3 and 4 fuse between each other and later they fuse with the urostyle (Fig. 13j).

Morphogenesis

The shape of the neurocranium at the early stages is rather compact as in the nototheniins. But the interorbital width in the trematomins is narrower, and the length of the ethmoidal region is longer than in the nototheniins. In *T. newnesi* and *P. borchgrevinki* the interorbital width increases during ontogeny. The width of the ethmoidal region simultaneously decreases, mainly in *P. borchgrevinki*. The highness of the ethmoidal region increases lesser than in the nototheniins, but on acccount for the sharp curvation of the anterior part of the parasphenoid dorsally the mesethmoid in *T. newnesi* and *P.*

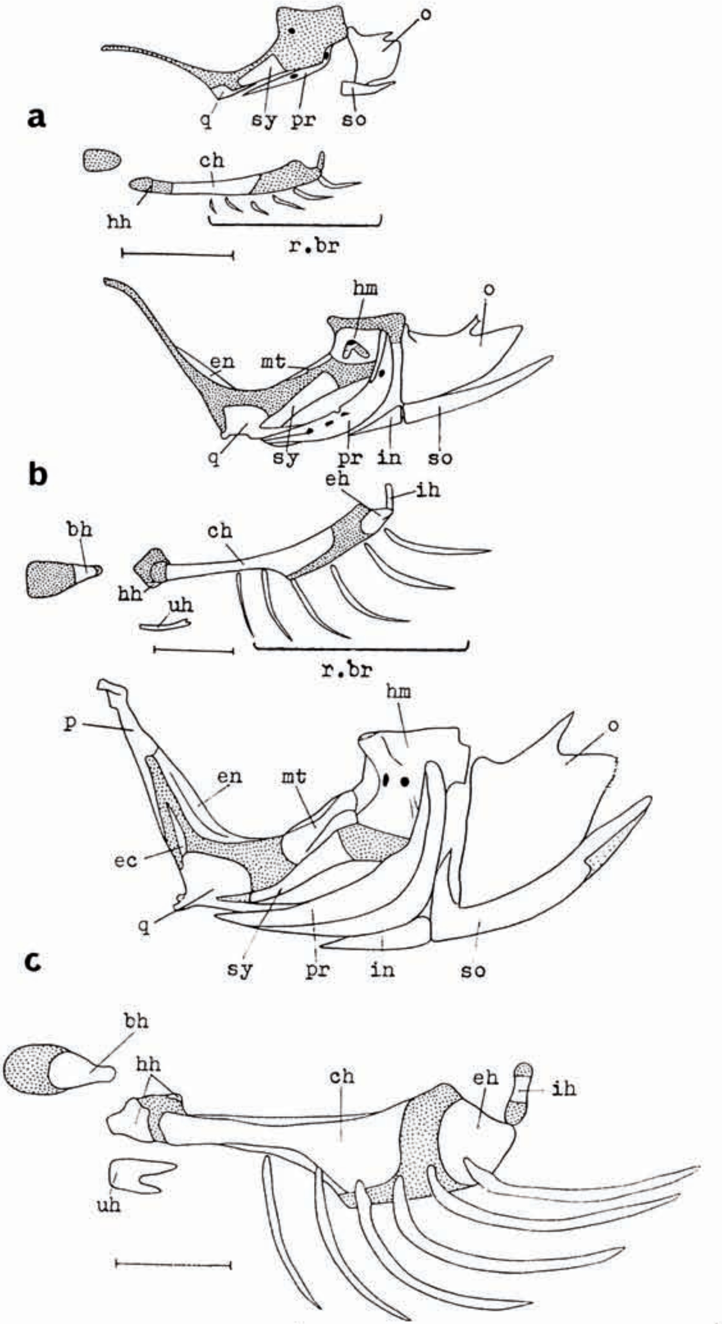


Fig. 11. - Development of the splanchnocranium in *Pseudotrematomus scotti*, left lateral views. Lengths of specimens as in figure 9. The labels as in figure 4.

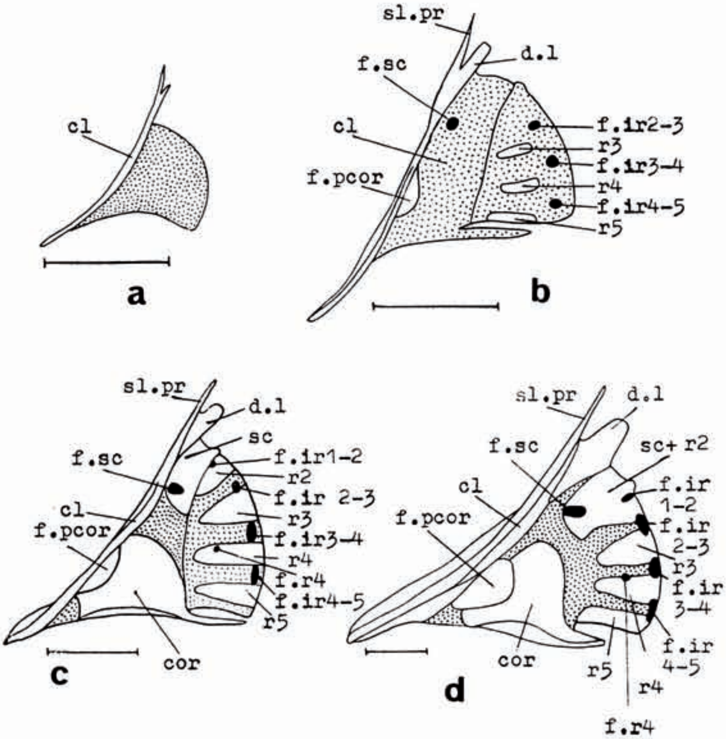


Fig. 12. - Development of the pectoral girdle and pectoral radials in *P. scotti*, left lateral views. Lengths of specimens are: (a) 19.5 mm, (b) 22.5 mm, (c) 28.0 mm, (d) 38.0 mm. The labels as in figure 7.

borchgrevinki some reachs the interorbital region. In *P. scotti* the interorbital width gradually decreases during ontogeny. At the early stages the interorbital region is strongly prominent and later gradually becomes lower, and the dorsal profile of the neurocranium is only slightly prominent in adults as in other trematomins. Simultaneously, the supraorbital seismosensorial canals originally divided by the medial edges of the frontals become more closer to each other, and in adults of *P. scotti* they are neighbour. The inclination of the anterior limb of the parasphenoid in *P. scotti* is less sharp than in *T. newnesi* and *P. borchgrevinki*, and the mesethmoid does not reach above the interorbital region (Fig. 9h).

In comparison with the nototheniins all the studied trematomins at different stages of growth have less highness of the ethmoidal region and more extensive cartilaginous ethmoidal and occipital regions of the skull (Fig. 9h-k). Moreover, the trematomins are characterized by weaker development of the ascending process of the parasphenoid which does not participate in the formation of the trigeminal nerve foramen.

The shape of the splanchnocranium at the early stages is rather similar in all three species of the trematomins. The most significant differences at that stages are found in the structure of the premaxillary processes and basihyal. In *T. newnesi* a well developed postmaxillary process is present already at 22 mm SL, later its size enlarges and at 30 mm SL the bone gets its definite shape. *P. scotti* has the small postmaxillary and well developed ascending processes at 19.5 mm SL, in juveniles and adults the gradual en-

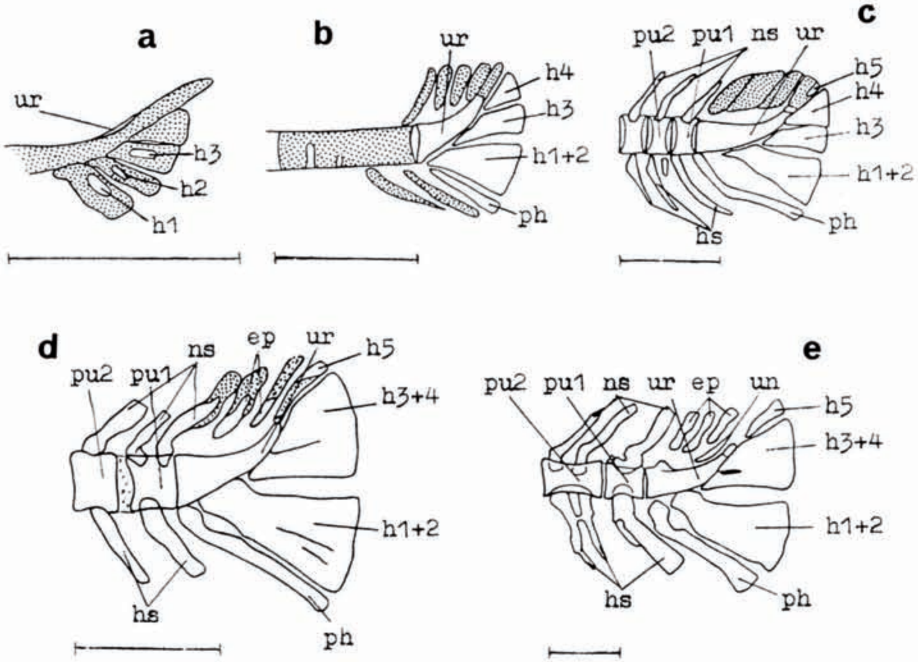


Fig. 13. - Development of the caudal skeleton in *Pseudotrematomus scotti*, left lateral views. Lengths of specimens as in figure 12. The labels as in figure 8.

largement of the ascending process and diminution of the postmaxillary process proceed (Fig. 10c). *P. borchgrevinki* at 34 mm SL has definite shape of the premaxilla with the moderate sizes of both processes. *T. newnesi*, rather early at 26 mm SL, gets the trapezium-like shape of the basihyal, both other species conserve a triangular shape of this bone during ontogeny.

Among the studied species of the trematomins *P. scotti* is characterized by the least changes of the shape of the splanchnocranium during ontogeny. In *T. newnesi* the highness of the quadrate, ento- and metapterygoids, hyomandibular and vertical limb of the preopercle increases considerably. The palatine becomes almost vertical, the bones of the hyoid arch lengthen very much. In *P. borchgrevinki* the highness of the suspensorium also enlarges and the palatine becomes more vertical, but not so much as in *T. newnesi*. The radial stripes of the edges of the opercular bones in *P. borchgrevinki* appears only in adults.

The development of the pectoral girdle in the trematomins is very similar to the nototheniins except for the development of the scapula (Fig. 12a-c). At the early stages the scapula surrounds the scapular foramen anteriorly and posteriorly, leaving its ventral edge free as in the nototheniins. Later, the posterior limb of the scapula grows anteriorly and borders the ventral edge of the scapular foramen, after that it joins the anterior limb of the bone (Fig. 12).

The dorsal end of the cleithrum, forming the spine-like process, is very long at the early stages in all the studied species of trematomins as in the nototheniins. After the appearance of the posterior lamella of the cleitrum the spine-like process strongly

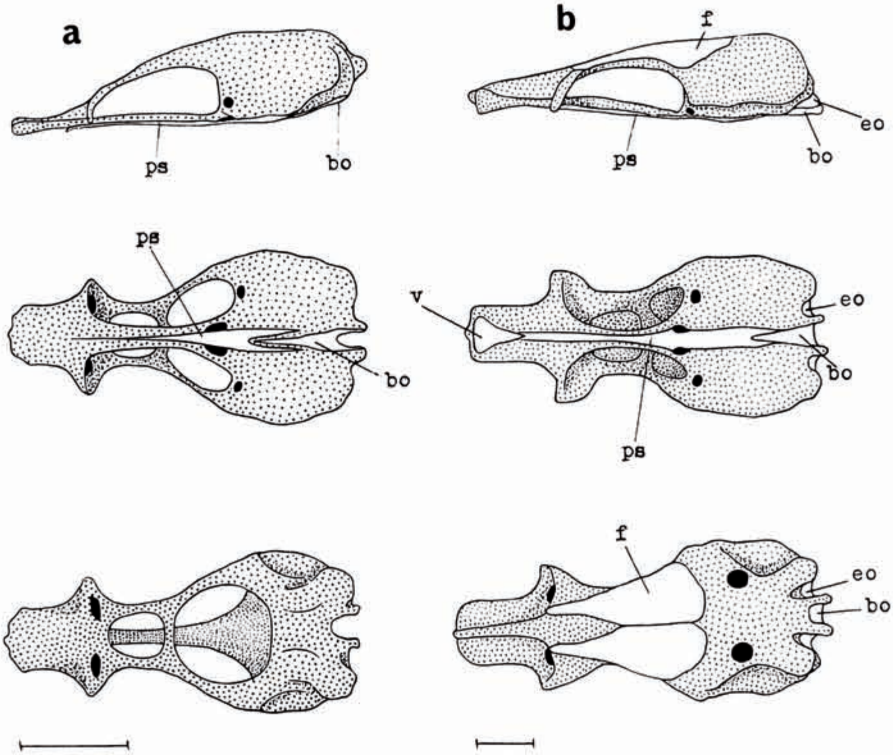


Fig. 14. - Development of the neurocranium in *Aethotaxis mitopteryx*, showing dorsal (bottom), ventral (middle) and left lateral (upper) views. Standard lengths of specimens are (a) 21.5 mm; (b) 36.0 mm. The labels as in figure 1.

diminutes and in adult trematomins is about the half of the length of the posterior lamella (Fig. 12).

The appearance of the vertebral centra of the trematomins differs of the nototheniins. They begin at the bases of the haemal archs, after that at the bases of the neural archs after that dorsal and ventral ossifications fuse at the lateral surface of the notochord.

Subfamily Pleuragramminae

The osteological development of larvae of *A. mitopteryx* was studied from 13 mm to 36 mm SL, being the maximal available size which was compared with the structure of adults.

Sequence of appearance of bones

At the early stages the sequence of appearance of bony elements of *A. mitopteryx* corresponds to those in nototheniins and trematomins (Fig. 14) in general. In contrast to other species, the basioccipital appears at the anterior edge of the rather deep notch of

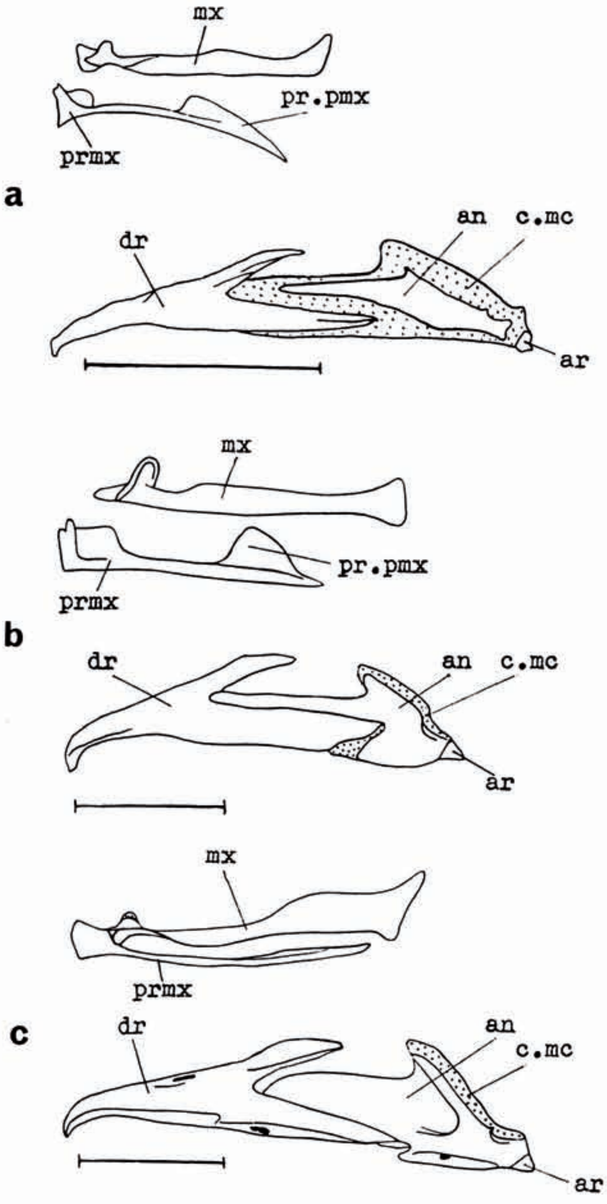


Fig. 15. - Development of the jaws in *Aethotaxis mitopteryx*, left lateral views. Lengths of specimens are: (a) 21.5 mm, (b) 27.0 mm, (c) 36.0 mm. The labels as in figure 3.

the cartilaginous vault of the skull (Fig. 14b), in which the anterior end of the notochord situates. It is noted also the very small length of the frontal, a feature which remains in adults also.

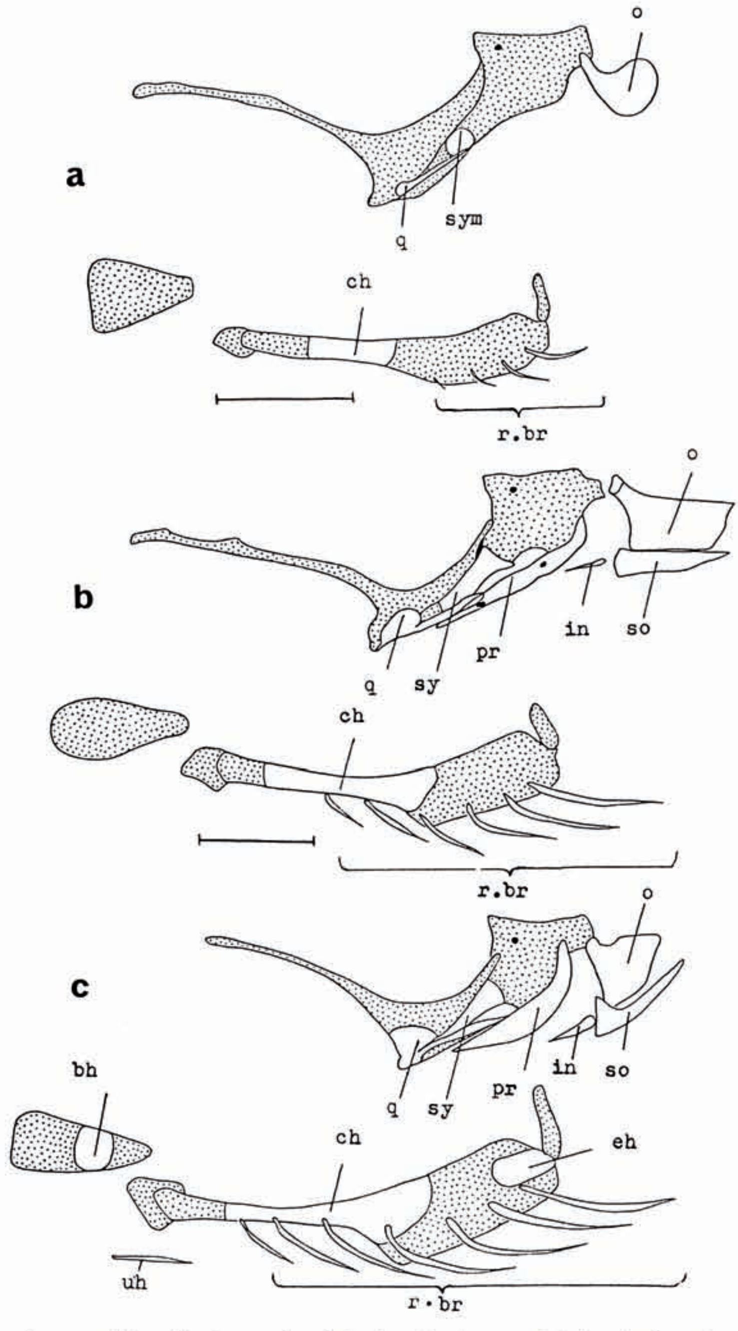


Fig. 16. - Development of the splanchnocranium in *Aethotaxis mitopteryx*, left lateral views. Lengths of specimens as in figure 15. The labels as in figure 4.

The sequence of appearance of bones of the splanchnocranium in general repeats that described for nototheniins and trematomins (Figs 15-17).

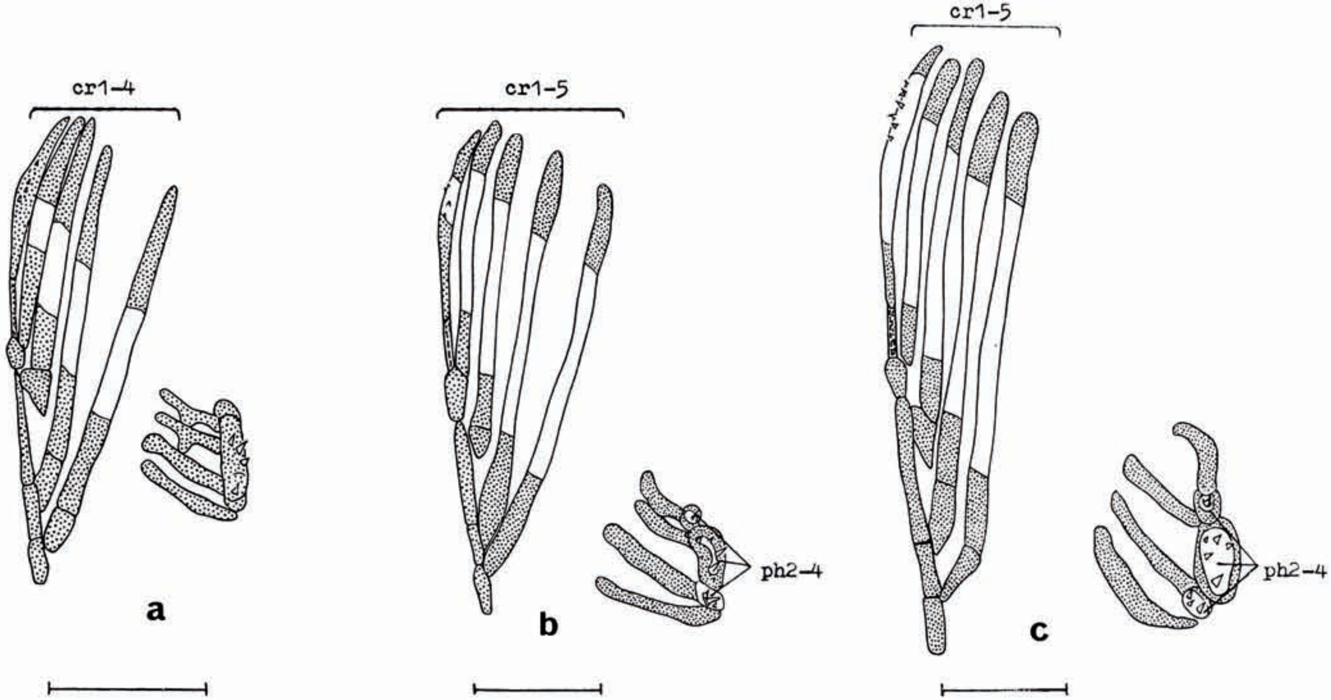


Fig. 17. - Development of the branchial skeleton of *Aethotaxis mitopteryx*, dorsal views for ventral parts of arches, ventral views for dorsal parts of arches. Lengths of specimens as in figure 15. The labels as in figure 6.

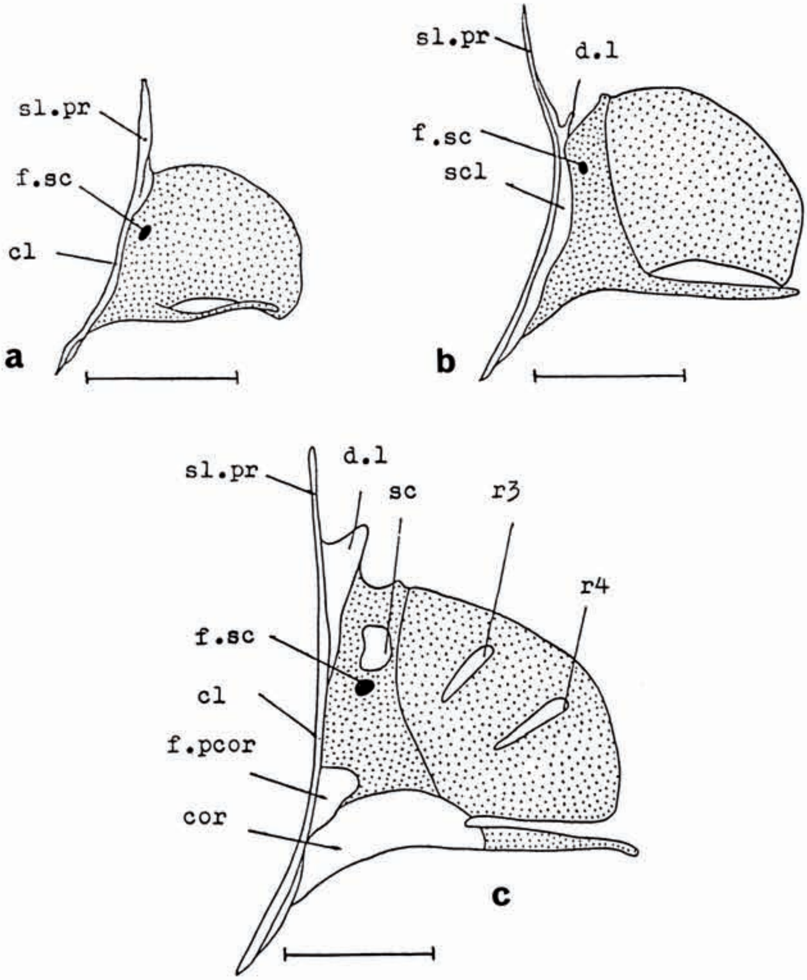


Fig. 18. - Development of the pectoral girdle and pectoral radials in *Aethotaxis mitopteryx*, left lateral views. Lengths of specimens as in figure 15. The labels as in figure 7.

Among the infraorbitals, the lacrimal appears at 27 mm SL. Other infraorbitals occur in specimens over 36 mm SL. In adults, the structure of the infraorbitals is similar to that in other nototheniids except for the strong reduction of the bony roof of the seismosensorial canal (DeWitt, 1962).

In the pectoral girdle the appearance of the coracoid and scapula precedes that of the radials 2 and 5 and occurs simultaneously with that of the radials 4 and 3 (Fig. 18). At 36 mm SL the interradial foramina are not present yet. In adults of *A. mitopteryx* the interradial foramina 1 and 2 are placed between radials 3-4 and 4-5.

As in the nototheniins and trematomins, the ossification of the vertebral column begins from the basioccipital posteriorly and from the urostyle. At 36 mm SL there are five free bony hypurals and parhypural, and two haemal and neural arches of the preural

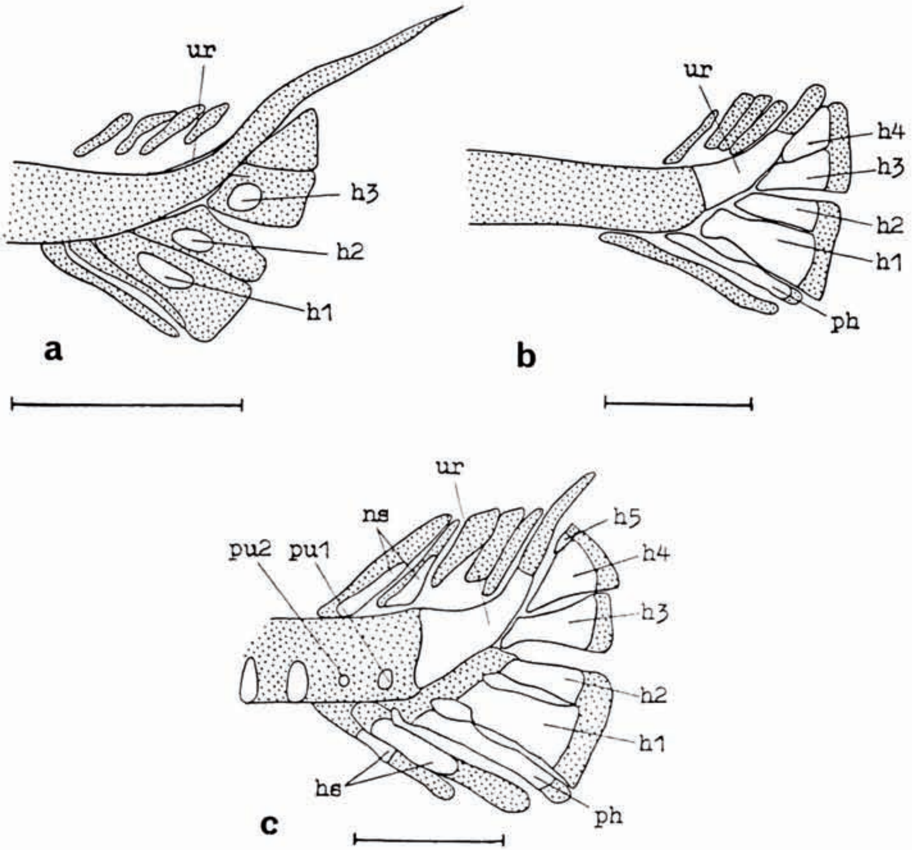


Fig. 19. - Development of the caudal skeleton in *Aethotaxis mitopteryx*, left lateral views. Lengths of specimens as in figure 15. The labels as in figure 8.

centra 1 and 2. All vertebral centra are present but some posterior haemal and neural arches are not ossified yet.

Morphogenesis

At the early stages *A. mitopteryx* has a direct ventral profile of the skull; at 36 mm SL its anterior end curves a little dorsally, and in adults forms the sharp inclination as in *T. newnesi* and *P. borchgrevinki*. The dorsal profile of the skull, previously prominent at the interorbital region, becomes more and more straight during the increase of highness of the ethmoidal region and in adults forms deep notch at the interorbital region. The interorbital width of larvae of *A. mitopteryx* is similar to that of trematomins. The ethmoidal region is very low and elongate, the vault of the skull is elongate too (Fig. 14). During ontogeny the gradual enlargement of the interorbital space and vault of the skull and the elongation of the ethmoidal region proceed. The horizontal limb of the lateral ethmoid is weakly developed in larvae of *A. mitopteryx* and the large cartilaginous regions remain between the lateral ethmoid and mesethmoid and also between the anterior ends of the frontals in adults. The ascending process of the parasphenoid is not well developed in larvae as well as in adults.

Major differences in the shape of bones of the splanchnocranium of *A. mitopteryx* and other nototheniids are revealed already at the early stages. Larvae of 27 mm SL has very long jaws, well developed articulary and postmaxillary processes and has no ascending process of the premaxilla. The shape of the jaws at 36 mm SL is similar to that in adults (Voskoboinikova, 1986). At 27 mm SL the suspensorium is low with the slope anterior end which is considerably lengthened (Fig. 16). The posterior process of the quadrate is well developed and lengthened as also the opercle which has no dorsal process until 36 mm SL. In adults the posterior process of the quadrate enlarges in the anterior part, the opercle remains long shape with a small dorsal process, the palate takes more vertical position conserving considerable length (Voskoboinikova, 1982, 1986). The gill arches are also longer than in other nototheniids in larvae and adults of *A. mitopteryx* (Fig. 17).

The specific character of the pectoral girdle of *A. mitopteryx* is the position of the base of the dorso-posterior lamella of cleithrum which is situated above the level of the dorsal edge of the primary pectoral girdle (Fig. 18) as in *Pleuragramma antarcticum* (Regan) (Voskoboinikova *et al.*, 1994). During ontogeny this base gradually goes down at the level of the dorsal edge of the scapula.

In the axial skeleton the formation of the vertebral centra proceeds in the same manner as that in the trematomins.

DISCUSSION

In general, all the studied species of the nototheniids, except *P. antarcticum*, are characterized by the similar sequence of appearance of the different bones (Voskoboinikova and Tereshchuk, 1991; Voskoboinikova *et al.*, 1994). The parasphenoid, basi- and exoccipital and posttemporal in the neurocranium; the maxilla, dentary, premaxilla, quadrate, quadratojugale, symplectic, ventral hypohyal, ceratohyal, branchiostegals, opercular bones and ceratobranchials in the splanchnocranium; the lacrimal in the infraorbitals; the cleithrum and supracleithrum in the pectoral girdle; the urostyle and anterior abdominal vertebrae in the axial skeleton are characterized by their earliest appearance. Contrarily, the basisphenoid, intercalar, pterosphenoid, supraoccipital, mesethmoid and lateral ethmoid in the neurocranium; the upper hypohyal, ectopterygoid, hypobranchial 3, basibranchials 1 and 2 in the splanchnocranium; the infraorbitals 2 and 3 in the infraorbitals; the scapula, coracoid and radial 2 in the pectoral girdle; hypural 5, epurals and uroneural in the caudal skeleton appear latest.

In *P. antarcticum* the basi- and exoccipital appear later than the parasphenoid and the axial skeleton has three centra of ossification: at the urostyle, at the basioccipital and at the level of the latest dorsal fin rays (Voskoboinikova *et al.*, 1994).

In general, the sequence of appearance of earliest bones of the nototheniids accords to that in other perciforms (e.g., Mook, 1977; Watson, 1982; Kohno and Taki, 1983; Karrer, 1984; Matsooka, 1985; Potthoff *et al.*, 1986, 1988; Peters, 1983). We agree with Weisell (1967) that the earliest ossifications occur in the most functionally important regions respondent for the compensation of hydrostatic pressure, feeding, breathing and movement of larvae.

The latest bones to ossify, as a rule, are characterized by the significant variability of shape or often, by the total reduction in the specialized species of the nototheniids or/and in the advanced families of the notothenioids. The basiphenoid in the genera *No-*

tothenia, *Paranotothenia* and *Dissostichus* of the nototheniids is very small. Because of this, Gosline (1968) and Balushkin (1989) interpreted the basisphenoid to be absent in this genera. Among other nototheniids, *P. antarcticum* and *A. mitopteryx*, belonging to the most specialized subfamily Pleuragramminae, do not have a basisphenoid. The advanced families Artedidraconidae, Bathydraconidae and Channichthyidae also lack a basisphenoid (Iwami, 1985).

The intercalar is well developed in the nototheniids and articulates with the prootic except in *A. mitopteryx* in which this articulation is lost. In the advanced species of the family Bathydraconidae (Voskoboinikova, 1988a) this bone is diminished and looses the articulation with the prootic. The size of the pterosphenoid is small in the bathydraconids and channichthyids (Iwami, 1985) and in the most advanced genera of the channichthyids this bone looses its articulation with the ascending process of the parasphenoid (which also becomes very small) causing the disappearance of the separate foramen of the trigeminal nerve.

The mesethmoid and lateral ethmoid are well developed in the nototheniins, in the trematomins they are small (Balushkin, 1982, 1989) as also in the pleuragrammins (Voskoboinikova *et al.*, 1984) where the broad bars of cartilage remain between them. Reduction in size of this bones is also shown in the bathydraconids (Iwami, 1985; Voskoboinikova, 1988b; Andriashev *et al.*, 1989) and in the channichthyids (Iwami, 1985).

Reduction of the upper hypohyal, basibranchials 1, 2 and pterygoids in the splanchnocranium is noted in species of the bathydraconids and channichthyids (Iwami and Abe, 1984; Iwami, 1985; Voskoboinikova, 1986).

Late ossification and articulation to each other of the infraorbitals 2 and 3 are also reflected in the hypothesized phylogeny of the notothenioids. These bones are separated in adults of *P. bernacchii*, *P. hansoni*, *P. nicolai* among nototheniids (Jakubowski, 1970; Andersen, 1984); *Gymnodraco acuticeps* (Voskoboinikova, 1988a), *Gerlachea australis* and *Cygnodraco mawsoni* in the bathydraconids. In the advanced species of the nototheniids *P. borchgrevinki*, *P. antarcticum* (Andriashev and Jakubowski, 1971; Jakubowski, 1971) and of the bathydraconids *Psilodraco breviceps* (Voskoboinikova, 1988b) the infraorbitalia 2 and 3 are lost.

In the pectoral girdle of nototheniids one of the latest bones to ossify is the scapula. The scapula is characterized by a considerable variability in shape and position of the scapular foramen (Boulenger, 1902; Pappenheim, 1914; Regan, 1913, 1914; Norman, 1938; Balushkin, 1989). In contrast to previous authors, Balushkin (1989) considered the scapular foramen positioned between the scapula and coracoid as an ancestral feature of the nototheniids. As our results shows, the formation of the scapular foramen proceeds at the latest stages of the development of the scapula. On one hand, it seems natural to decide that the appearance of the open scapular foramen in the nototheniins is correlated with reduction of the ventral part of the scapula because the process of reduction of ossification plays an important role in evolution of the notothenioids (e.g., Iwami, 1985; Voskoboinikova, 1986). On the other hand, based on the fact that the development of the pectoral girdle is best in the nototheniins, and the ossification of the ventral part of the scapula in the trematomins and pleuragrammins is obviously correlated with reduction of ossification of the coracoid, and in particular, its dorsal edge, it is possible to propose that the formation of the closed foramen in this subfamilies can be considered as the derived character.

Among the bones of caudal skeleton of the nototheniids, the hypural 5, epurals and uroneural appear latest. The hypural 5 and uroneural are absent in *P. antarcticum*

(Totton, 1914; Andersen, 1984; Voskoboinikova *et al.*, 1994), in *P. breviceps* and *G. acuticeps* of the bathydraconids (Andriashev *et al.*, 1989; Balushkin and Voskoboinikova, 1995) and in the channichthyids (Iwami, 1985). The number of the epurals varies in *P. antarcticum* (Voskoboinikova *et al.*, 1994) and in the harpagiferids, bathydraconids and channichthyids (Iwami, 1985).

The investigation of the morphogenesis of certain bones of the nototheniids gives the possibility to follow the appearance of some systematic characters in ontogeny and establish their polarization in phylogeny. All the studied species of the nototheniins and trematomins are characterized at the early stages by rather compact shape of the neurocranium with the relatively broad and short ethmoidal region, broad interorbital width, prominent dorsal and slightly prominent ventral profile of the skull. The described features are generalized in nototheniids and probably are primitive in the group. The similar conclusion was drawn by Balushkin (1989) based on adult nototheniid neurocranium structure. The shape of the neurocranium of the pleuragrammins differs from that of the nototheniids already at the early stages. In both studied species of this subfamily the neurocranium is rather elongate with long and low ethmoidal region, rather broad interorbital region, prominent dorsal and direct ventral profiles of the skull. That features can be interpreted as advanced.

Among the nototheniins, *N. neglecta* conserves the described primitive shape of the neurocranium throughout life without significant changes. Other studied species of the nototheniins are characterized by the diminution of the interorbital space, lengthening of the ethmoidal region and enlargement of the anterior inclination of the ethmoidal region in ontogeny. Among four examined species of the nototheniins it is possible to separate two groups, characterized by similar modifications of the neurocranium shape during ontogeny: *L. nudifrons-G. gibberifrons* and *L. kempi-N. larseni*. First two species obtain the highest anterior inclination of the ethmoidal region and narrowest interorbital space during ontogeny, in adults of *G. gibberifrons* these characters being developed more strongly in comparison with *L. nudifrons* (Balushkin, 1984). *L. kempi* and, in particular *N. larseni*, having already at early stages of development some advanced characters (the elongate and low ethmoidal region and rather narrow interorbital space) mainly conserve these larval characters during ontogeny (Balushkin, 1989) in contrast to first group.

Among the trematomins, two group of species can be recognized based on the modification of the neurocranium. *P. scotti* and *P. eulepidotus* reveal during ontogeny the relative persistance or diminution of the length of the ethmoidal region, considerable diminution of the breadth of the interorbital space, persistance of the prominent dorsal and ventral profiles of the skull. Contrarily, *T. newnesi* and *P. borchgrevinki* are characterized by the development of the longest ethmoidal region, broadened interorbital space, direct dorsal and strongly prominent ventral profiles of the skull.

The pleuragrammins also show two different types of development of the neurocranium. In *A. mitopteryx* during ontogeny the lengthening of the ethmoidal region, enlargement of the interorbital space, appearance of the nothch in the dorsal profile and strong prominence of the ventral profile proceed. In *P. antarcticum* the ethmoidal region conserves its length, also does the interorbital space, the dorsal profile becomes straight and the ventral one becomes strongly prominent as in the previous species (Voskoboinikova *et al.*, 1994).

The splanchnocranium of the studied nototheniids also have some general peculiarities of the structure at the early stages. These are the small highness of the suspensorium, sloping position of the anterior limb of the palatoquadrate cartilage, direct shape and vertical position of the preopercle, moderate length of the jaws. Analyzing the structure of the splanchnocranium of adult nototheniids some authors (e.g., Balushkin and Voskoboinikova, 1979; Voskoboinikova, 1986) concluded that the most close to the ancestral form in the structure of the splanchnocranium are *Eleginops maclovinus* Val. recently separated in more primitive subfamily Eleginopsidae (Balushkin, 1992) and *Gobionotothen angustifrons* (Fisher) which also are characterized by the low suspensorium and sloping position of the palate. Moreover, *Pseudaphritis urvilli* Cuv. which is considered by some authors as sister group to rest notothenioids (Balushkin, 1992; Ritchie *et al.*, in press) also has similar structure of the splanchnocranium (Voskoboinikova, 1986). So, probably, described characters can be considered as the ancestral for the nototheniids.

Among the studied nototheniins, *G. gibberifrons*, *N. neglecta* and *N. larseni* obtain the most specialized characters of the structure of the spanchnocranium during growth. So, *G. gibberifrons* conserves small highness of the suspensorium in a difference from other species where the highness of the suspensorium essentially enlarges on account for the development of the ventral process of the hyomandibular and vertical limb of the preopercle. As advanced characters of *G. gibberifrons* it is possible to mention the enlargement of bones in the horizontal direction and appearance of the blunt and curved teeth on the shortened jaws. *N. neglecta* differs from other species of nototheniins by the strong enlargement of most bones and the canine-like teeth (Voskoboinikova, 1986). *N. larseni* is characterized by the weak development of the pterygoids, anterior edges of the hyomandibular and preopercle and the villiform teeth.

Among trematomins, *P. scotti* conserves the larval shape of the splanchnocranium. In *T. newnesi*, *P. borchgrevinki*, and *P. eulepidotus* (Voskoboinikova and Tereshchuk, 1991) the enlargement of the highness of the suspensorium proceeds. The position of the palatine becomes more vertical. *T. newnesi* gets the most advanced characters such as the largest high of the palatine, quadrate, ento- and metapterygoids, hyomandibular, vertical limb of the preopercle, trapezoidal shape of the basihyal, the lengthening of jaws and hyoid arch.

The pleuragrammins retain during ontogeny some juvenile characters: the weak development of the pterygoids, interstial part of the preopercle, dorsal process of the opercle and the presence of the villiform teeth. But such advanced characters as the significant length of the palatoquadrate cartilage, posterior process of the quadrate, operculum, hyoid and gill arches (Voskoboinikova, 1986) appear already at the early stages and are conserved during ontogeny.

At the early stages of the development of the pectoral girdle in the nototheniids, the cleithrum has the well developed dorsal limb which later transforms in a spine-like process gradually diminishing, while the dorso-posterior lobe of the bone develops. During ontogeny of nototheniins and trematomins the bases of the spine-like process and dorsoposterior lobe are situated at the dorsal edge of the scapula. At the early stages in the pleuragrammins the cleithrum has very high dorsal limb, and the bases of the spine-like process and dorso-posterior lobe situate above the dorsal edge of the scapula. *P. antarcticum* conserves this structure of cleithrum in adults (Voskoboinikova *et al.*, 1994), and *A. mitopteryx* obtains structure usual for other nototheniids.

All the studied species of the nototheniids are characterized by the appearance of four free bony radials in the pectoral girdle of which the dorsal radial (r2) later fuses to the scapula. The existence of three free radials is the diagnostic character of the suborder Notothenioidei (Regan, 1913; Norman, 1938). Some authors (Gregory, 1933; Balushkin,

1989) note the complex nature of the scapula of the notothenioids formed by the fusion of two most dorsal radials with this bone based on the number of proposed interradial foramina in the scapula. Free cartilaginous very small radial first (r1) was found only once in larvae of *Pseudotrematomus loennbergi* of 19 mm SL. Probaly, later this radial fuses with cartilaginous primary pectoral girdle. However, the fusion of radial second with the scapula during ontogeny is usual process for all the studied nototheniids. So, result of our study supports the point of view of Gregory and Balushkin.

It was shown for the nototheniids (Balushkin, 1989) that the number of the interradial foramina tends to be reduced. Balushkin proposed that at the early stages of ontogeny in the nototheniids the appearance of five interradial foramina proceeds which later are closed in a different degree in different species. It is obviously from our study that in the nototheniins the number of the appearing foramina corresponds to the number in adults. Foramina between the radials 3-4 and 4-5 present in adults of all five studied species appear earlier than foramina between the radials 2-3 (*G. gibberifrons*) and 1-2 occurring in larvae and adults of *L. nudifrons*, *L. kempi* and *N. larseni* only. In other nototheniids (except for *T. newnesi*) five interradial foramina appear from which the foramen 2-3 can be closed during ontogeny in *P. scotti* and *P. borchgrevinki*, and the foramina 1-2, 2-3 and 3-4 are closed during ontogeny in *P. antarcticum* (Voskoboinikova *et al.*, 1994) and probably *A. mitopteryx*. The sequence of appearance of the interradial foramina in this species goes in the dorsal direction and corresponds to the appearance of free bony radials (r 4, 3, 5, 2) and scapula. Contrarily, the lack of the interradial foramina during ontogeny proceeds in ventral direction. We propose that the first stage of interradial foramina formation in nototheniids is the absence of any foramina in ontogeny (trematomins, pleuragrammins), and a second stage is the appearance of the foramina in ontogeny (nototheniins).

Balushkin (1974, 1989) based on Totton's (1914) conclusion about the fusion of the hypurals in ontogeny of *P. antarcticum* postulated that the development of the hypurals in ontogeny corresponds to their development in phylogeny of the notothenioids. Our results also show the fusion of the hypurals in ontogeny of the nototheniids which however proceeds at different stages in different species. In the most of the studied species of the nototheniids the number of appearing bony hypurals corresponds to the number of the cartilaginous hypurals and fusion proceeds between the bony hypurals 1 and 2 (in the nototheniins and trematomins) and 3 and 4 (sometimes in *L. kempi* and always in *G. gibberifrons* and trematomins). In *G. gibberifrons* and *P. antarcticum* (Totton, 1914; Voskoboinikova *et al.*, 1994) the fusion of the cartilaginous hypurals 1 and 2 proceeds and one bony hypural 1 + 2 appears. Both species are characterized by the most advanced structure of the caudal skeleton (Balushkin, 1974, 1989) that, probably, could be considered as phenomena of the predisplacement of this structure in ontogeny (McNamara, 1986).

The present data on the osteological development of the nototheniids, in general agree with those of the previous researchers (Andersen and Hureau, 1979; Andersen, 1984; Balushkin, 1982, 1989; DeWitt *et al.*, 1990; Balushkin, 1992) on the existence of three valid subfamilies Nototheniinae, Trematominae and Pleuragramminae in the family Nototheniidae, the species of which are recognized not only by the morphological characters of adults, but also by morphogenetic characters concerning the development of the neurocranium, splanchnocranium, pectoral girdle and axial skeleton. It is shown that among these three subfamilies the nototheniins bears at early stage the most of primitive characters. In contrast, trematomins and mostly pleuragrammins are characterized by advanced features already at the early stages of development.

Among the nototheniins *N. neglecta* conserves during ontogeny the juvenile and possibly primitive shape of the neurocranium together with very advanced characters of the splanchnocranium. Among members of the subfamily this species shows an independent way of osteological development. Among other four species (*G. gibberifrons*, *L. nudifrons*, *L. kempi* and *N. larseni*) of the nototheniins it is possible to note two lines of the osteological development: (1) *L. nudifrons* and *G. gibberifrons* are characterized by the diminition of the interorbital width and high inclination of the ethmoidal region, *G. gibberifrons* bears such advanced characters as the horizontal broadening of the bones of the splanchnocranium and heterochrony (predisplacement) in the development of the hypurals; and (2) *L. kempi*-*N. larseni* conserving some juvenile characters such as the lengthening of the ethmoidal region and moderate breadth of the interorbital space of the neurocranium; *N. larseni* also reveals some retardation in the development of bones of the splanchnocranium.

Among the trematomins two lines of the osteological development are recognized: (1) *T. newnesi*-*P. borchgrevinki* are characterized by the enlargement of the interorbital width and appearance of the straight dorsal and strongly prominent ventral profiles of the skull; and (2) *P. scotti* and *P. eulepidotus* are characterized by the diminution of the interorbital width and conservation of sligthly prominent dorsal and ventral profiles of the skull.

The pleuragrammins well differ from each from other already at the early stages by heterochrony in the appearance of the occipital bones, vertebrae and hypurals which give to *P. antarcticum* some advanced characters in the structure of the neurocranium, infraorbitals, axial and caudal skeleton which separate this species not only from other pleuragrammins but also from other nototheniids. This is an argument to put *P. antarcticum* in a separate subfamily of the nototheniids.

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